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STYLIDIUM IN ARNHEM LAND: NEW SPECIES, MODES OF  
SPECIATION ON THE SANDSTONE PLATEAU, AND  
COMMENTS ON FLORAL MIMICRY

Sherwin Carlquist<sup>1</sup>

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Introduction

The northeastern portion of Northern Territory, Australia, is known as Arnhem Land. Arnhem Land can be defined in various ways, but the geographical feature I wish to use is the sandstone plateau, often termed the sandstone scarp. Areas very close to the sandstone scarp are also discussed in this paper. The plateau can be said to form a large triangle lying within Oenpelli on the northwest, Nhulunbuy (Gove Peninsula) on the northeast, and Mataranka (south of Katherine) on the south. The borders of the plateau are not easily definable, because isolated tablelands away from the main scarp are numerous in places and because the lower northeastern portions of the plateau may rise only a little above the lowlands. Although cut by dramatic gorges—most notably Katherine Gorge and the gorge of the East Alligator River—the plateau generally lies at only about 300 m (or 1,000 ft). Thus it is not climatically distinct from the lowlands, as are other sandstone plateaus in the world (the Guayana highlands of South America; the mountains of Cape Province, South Africa). Reasons why the Arnhem Land sandstone plateau is nevertheless interesting with respect to speciation in angiosperms are given below.

My interest in visiting the plateau was based upon my work with the family Stylidiaceae. In June of 1977, I acquainted myself with the *Stylidium* flora of Darwin and vicinity. Views of the plateau from a commercial flight convinced me that both the plateau and the interface between scarp and floodplain would be ideal places in which to find populations of *Stylidium*. Deposits of white sands and occurrence of streams or temporary standing water in conjunction with sand are ideal habitats for that genus.

The periphery of the plateau can be explored by road to a certain extent. Using such roads, one may climb the scarp and explore the surface of the plateau. Such access points are rather few, however. The only readily visited point is at Katherine Gorge National Park. However, a field biologist who has reached the scarp will find that the eroded sandstone terrain is rougher than what a map might suggest. Ordinary walking techniques or even use of pack animals permit one to penetrate only the fringes of this large plateau. Surface vehicles of any kind would reach impassable barriers and would be less successful than travel on foot.

An area of distinctive topography, suggesting inherent botanical interest yet with great difficulty of access, is likely to yield plant discoveries when exploration can be undertaken. The Australian-American Expedition to Arnhem Land (Specht 1958) did uncover a number of novelties, but the number may be considered moderate. In fact, the localities from which exploration was undertaken, Groote Eylandt, Bickerton Island, Yirkalla (now Nhulunbuy or Gove), Melville Bay, Port Bradshaw, and Oenpelli, are all off the plateau. Exploration of the edge of the scarp near Oenpelli was undertaken by that expedition, however. No novelties were discovered in *Stylidium* by that expedition, although some new records of occurrence for Arnhem Land were noted.

The plateau itself, with occasional exceptions, has remained relatively unexplored botanically. One must concede that the marked seasonality of Arnhem Land's rainfall renders this region poorer in species number than a comparable area of wet, stable rain forest or cloud forest. By the phrase "relatively unexplored botanically," one might assume that I refer to discovery of undescribed species. There are indeed taxonomic novelties to be expected, but one must stress that facts about ecology, anatomy, etc., of Arnhem Land plants are potentially more interesting.

The simplest means of access to the Arnhem Land sandstones as of the present date is helicopter. As described below, helicopter charter permitted visits to three sites on the plateau. Such visits are an extraordinary privilege. Quite conceivably, particular places on the plateau may well never have been seen by a human. Food sources for survival on the plateau by aborigines or others are much scarcer than in the lowlands adjacent to the scarp. The plateau has remained a remarkably intact wilderness area; virtually no plant weeds have entered, and the terrain has, in general, deterred the water buffalo, the only major vertebrate with destructive potential.

### Field Logistics, Materials, Acknowledgments

The great majority of *Stylidium* species in Northern Territory are annuals. As with other ephemeral annuals of the Territory, they respond closely in growth events to the timing of the monsoon rainfall. The progression may seem unexpected to those unfamiliar with this region. The monsoon rains fall chiefly between November and April. Many of the sandy depressions where *Stylidium* species grow may be filled or inundated during this period. For example, the lower rosettes on some plants of *S. curtum* (Fig. 18) or the succulent stems and elongate leaves of some populations of *S. muscicola* F. Muell. (Fig. 46) are formed below water. As the rains wane, temperatures also drop. Thus the growing season which terminates in flowering coincides with progressive cooling; however, at no time do frosts occur (in areas near the coast; in interior areas winter frosts are common). The absence of frost

renders a progressively cooler growing season no disadvantage. In fact, cooling slows evaporation of soil moisture, attenuating the growing season. The marked seasonality of rainfall in northern Australia results in relatively rapid drying of soils in any case. For annuals dependent on moisture near soil surfaces, flowering must occur roughly before mid-July. This regime alters slightly depending on the progression of the monsoons. In 1977, the monsoons were typical, ending during late April with flowering of ephemerals most abundant during the latter part of June. In 1978, however, the rains ceased in March. Mr. Clyde R. Dunlop, botanist with the Darwin Herbarium, notified me that flowering would be about a month earlier than in 1977. Because of this prediction (which proved to be correct), I scheduled my field work so that the Arnhem Land sandstone plateau could be seen during the first two weeks of June. Prior to plateau exploration, field work near the scarp in the vicinity of Jabiru and Koongarra was undertaken in company with Mr. Dunlop, whose knowledge of this area proved invaluable.

Beginning on June 2, three sites on the plateau were visited. By means of helicopter travel, sites were selected on the basis of a rapid decision as to suitability of the habitat for botanical interest and for camping. The three encampments were as follows:

Camp 1: 12°59' S., 133°9' E.

Camp 2: 13°4' S., 133° 1' E.

Camp 3: 12°41' S., 133°27' E.

These localities are given to the closest minute, and are approximate. Mr. Dunlop joined me on all three encampments, Mr. Tom Henshall of the Alice Springs Herbarium was present at encampments 2 and 3, and Mr. Peter K. Latz, also of that herbarium, was at encampment 3. I wish to express my thanks to these individuals, whose knowledge of Australian topography and botany proved very helpful. In particular, Mr. Dunlop was very helpful not only by sharing his knowledge, but by making equipment and supplies available.

The timing of these encampments proved exactly right for the rather dry 1978 conditions. Although many comparisons among the three sites could be made, I was most amazed at the great disparity of their respective floras: only a few species occurred at more than one of the three camps, despite occurrence of what seemed like the same range of microhabitats. This was quite striking in the case of the genus *Stylidium*. Two new species were found at Camp 1, a third at Camp 2. It seems quite unlikely that these two places, selected almost at random, should yield new species of *Stylidium*, yet no species be found on the plateau in the future: almost certainly there will be further novelties.

After the helicopter visits, I traveled to a more southerly portion of the plateau, Katherine Gorge National Park, by automobile. Because this place



is more than 200 km inland from the encampments just mentioned, the plateau at Katherine Gorge is drier. The plateau may be reached here by means of a trail which ascends from the park headquarters. This trail parallels the Gorge along its southern scarp. A walk of 7 km along this trail yielded an interesting assortment of *Stylidium*s, including a new species.

Visits to nonplateau areas of Northern Territory in 1977 and 1978 proved essential in understanding patterns of evolution in northern Australian *Stylidium*s. Most of these areas were along the Stuart Highway, within 30 km of Darwin. Sandy depressions, signaled by occurrence of *Pandanus*, proved richest in occurrence of *Stylidium*s. The areas around the suburb of Berri-mah proved especially rewarding. Nonplateau localities are cited below and, more in detail, in my earlier paper (Carlquist 1978).

Specimens, unless otherwise cited, are represented in the herbarium of the Rancho Santa Ana Botanic Garden. Replicates have been distributed to other herbaria. During my 1978 visit to Northern Territory, I determined the *Stylidium* specimens of the Darwin (DNA) and Alice Springs (NT) herbaria. In the latter collection, a specimen of Mr. D. E. Symon proved unusually interesting. I obtained a loan of *Stylidium* specimens, mostly from Northern Territory, from Mr. Symon's institute, the Waite Agricultural Institute, Glen Osmond, South Australia, and determined that collection. I am grateful to the curators of these herbaria for their kindness in making these materials available to me.

Documentation took the form of notes, still photographs of various magnifications both in color and in black-and-white, motion pictures of flowers to show trigger mechanisms, dried specimens, and pickled specimens.

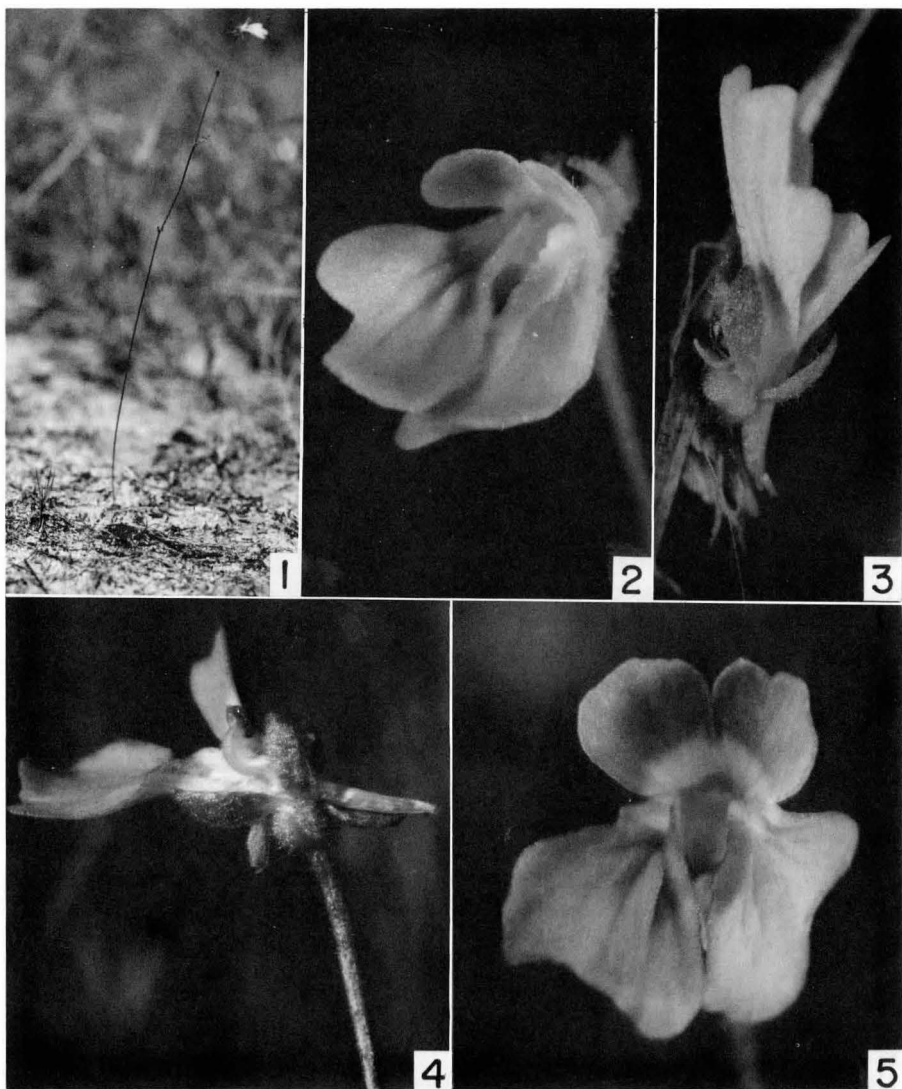
### Taxonomy

Before considering modes of speciation on the Arnhem Land plateau and surrounding regions, new species must be added to the Northern Territory flora. The reader who wishes to obtain a current picture of which species currently are reported from Northern Territory (and other parts of tropical Australia) should consult Erickson (1958), Erickson and Willis (1966) and Carlquist (1978).

*Stylidium longicornu* Carlquist, sp. nov.

Fig. 1-6, 89

Herba annua, pilis glanduligeris parce adspersa, imprimis in calycibus. Folia basalia rosulata, obovato-spathulata, 4-6 mm longa. Scapi tenuissimi filiformes, 10-30 cm alti, triente superiore bracteis 2 oppositis minutis instructi. Scapi dichasia unilateralia racemiformi efformantem gerentes. Pedicelli 2-3 cm longi, tenelli. Calycis tubus subglobosus, lobi paulo longiores nunc subaequales nunc anteriores 2 manifeste longiores et latiores quam 3



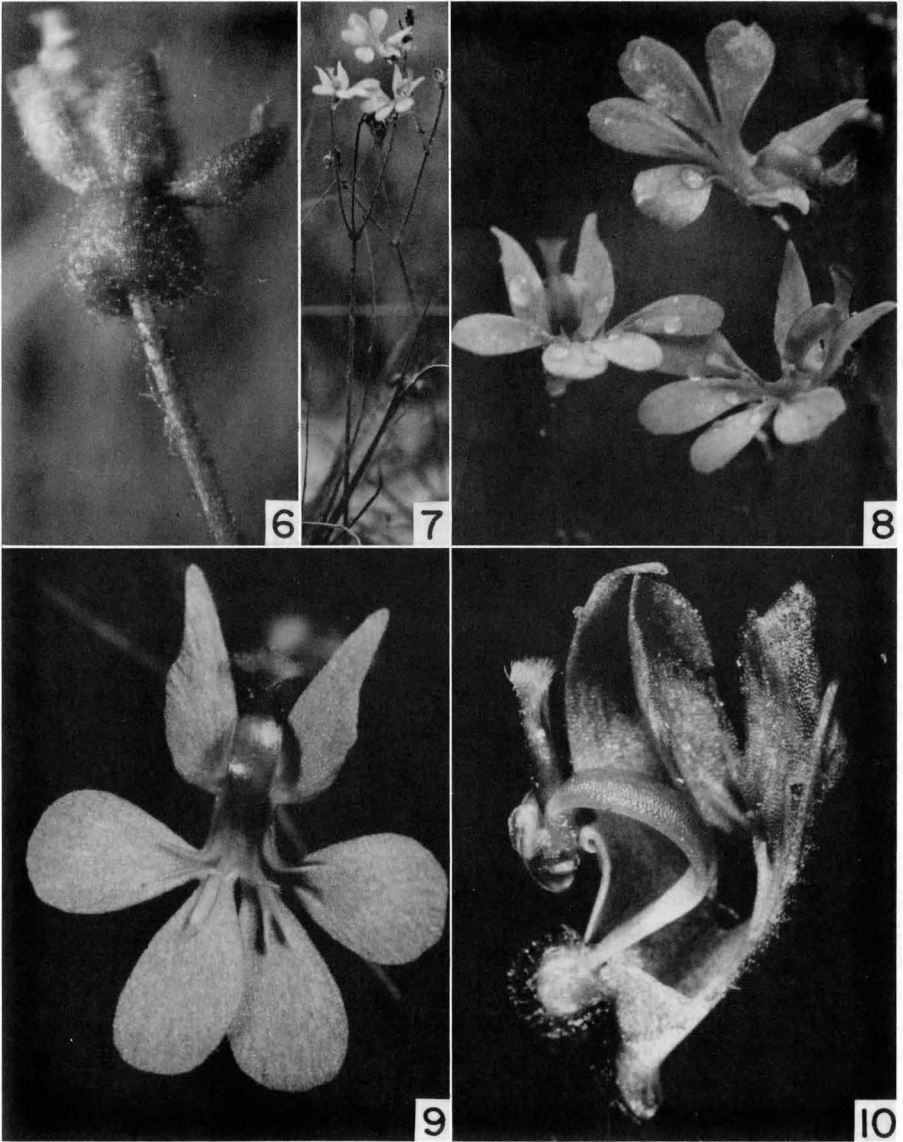
Figs. 1-5. *Stylidium longicornu* (Carlquist 15404).—1. Habit of plant at type locality.  $\times 1$ .—2-5. Closeups of flowers.  $\times 14$ . —2. Oblique face view of flower, showing the ridges of the lower corolla lobes where they outline the space through which the column operates.—3. Side view of flower, in nocturnal closed position. Flower is supported on herbage of another plant for convenience in photography.—4. Side view of flower, corolla lobes on side facing camera removed so that column is visible; labellum shows to left of ovary.—5. Corolla in face view.

posteriores lanceolati obtusiusculi; lobus medianus posticus paulo procalcarata. Corollae tubus perbrevis postice supra lobum calycinum medianum in calcar elongatum et calycis lobum duplo superans productus; laciniae inaequales, posteriores 2 rotundatae, violaceae set ad basi albae, rotundatae, 2–3 mm longae; laciniae 2 anteriores quam posteriores duplo longiores, irregulariter spathulatae, violaceae, ovata-acuminatae, margine interiore carinata. Labellum 0.5 mm longum. Faux nuda. Columna fere ut in *S. calcarato* formata sed breviora, 1.5–2 mm longa. Capsula ovata-globosa 2 mm longa. Semina minuta.

Annual herb with scattered glandular hairs, most notably on ovary and on calyx lobes. Leaves in a basal rosette, obovate-spathulate, 4–6 mm long. Scapes filiform, very slender, 10–30 cm tall, provided with pairs of small opposite bracts in the upper third. Inflorescences are unbranched racemes which represent modifications from a dichasial cyme to a unilateral cyme, main axis not perfectly straight but zigzag. Pedicels slender, 2–3 cm long. Ovary subglobose, calyx lobes of two lengths, the anterior pair longer and wider than the posterior three, lanceolate and obtuse; median lobe subtending the spur. Corolla tube very short, posteriorly bearing an elongate spur almost twice as long as the calyx lobe subtending it. Corolla lobes unequal, the posterior pair circular in outline, about 2–3 mm long, violet but white at bases; anterior pair of lobes twice as long as the posterior ones, 4–6 mm long, irregularly spathulate, violet (paler outside), interior margin (sinus) ridged; inner surface of corolla lobes grooved where veins occur. Throat without appendages. Labellum 0.5–1.0 mm long, ovate-acuminate. Column morphology and disposition as in *S. calcaratum* but smaller, 1.5–2 mm long. Capsule ovate-globose, 2 mm long. Seeds minute.

*Holotype*.—Among drying *Rhynchospora*, grasses, and occasional plants of *Styliidium lobuliflorum* F. Muell. on a white sand flat where clumps of *Leptocarpus* grow, near sandstone blocks where one can find *Grevillea*, *Melaleuca*, *Blepharocarya*, and *Verticordia*. Camp 1, Arnhem Land, Northern Territory. June 3, 1978. *Carlquist 15404* (RSA). *Isotypes*.—DNA, PERTH, US.

Although individuals of this species were occasional at various points in the vicinity of Camp 1, I have not collected or seen collections of this species elsewhere. *Styliidium longicornu* may be expected in other localities, however. Indeed, there is a hint that Erickson (1958) may have seen this plant. In his description of *S. ceratophorum*, Schwarz (1927) describes precisely the plant I have illustrated in figures 7–10, a plant quite different from *S. longicornu*. The flowers are orange ("deep yellow" according to Schwarz, who saw dried material only), the prominent yellow bifid throat appendages (Fig. 9) exactly as he described them. Schwarz makes no mention of alternative flower color. However, Erickson's (1958) description of *S. ceratophorum* reads "golden-yellowish or mauve with a white throat."



Figs. 6–10. *Stylidium* flowers and flower parts.—6. *S. longicornu* (Carlquist 15404). Ovary maturing into fruit.  $\times 20$ .—7–10. *S. ceratophorum* (Carlquist 15385).—7. Habit of plant.  $\times 7$ .—8. Three flowers, bearing raindrops. Column poised on all flowers.  $\times 2.5$ .—9. Flower in normal position, face view. Column poised.  $\times 3.5$ .—10. Flower cut longitudinally; spur intact. The column and its stigma can be seen clearly in this dissection.  $\times 3.5$ .

The latter suggests *S. longicornu*, although Erickson gives no details that do not correspond to typical *S. ceratophorum* in her description. In several places in her 1958 book, Erickson noted variants of known species. Some of these variants proved to be new species, such as *S. aeonioides* S. Carlquist and *S. arenicola* S. Carlquist (Carlquist 1969).

Although *S. longicornu* is markedly different from *S. ceratophorum*, as will be noted below, the two both do belong to the subgenus *Centridium* Lindl. as delimited by Mildbraed (1908). Schwarz (1927) was dubious as to which subgenus *S. ceratophorum*, which he described, should belong, *Centridium* or *Andersonia* G. Koenig. *Centridium* is the correct choice. Two species of southwestern Australia, *S. calcaratum* R. Br. and *S. perpusillum* Hook f., belong to subgenus *Centridium*.

All four species of *Centridium* have a distinctive spur (Fig. 3, 4, 10), a long-stipitate stigma (Fig. 10, upper left), a spherical ovary (and capsule), and the ability—not found elsewhere in *Stylidium* but characteristic of the genus *Levenhookia*—to close flowers at night. Although the column is basically the same in all four species, the two tropical species, *S. ceratophorum* and *S. longicornu*, lack the prominent tooth midway along the column possessed by the two southwestern Australian species. This suggests the tropical species may be closer to each other than either is to the southwestern species.

The two tropical species are amply distinct from each other, however. As noted by Erickson (1958) and Carlquist (1969), *S. calcaratum* and *S. perpusillum* have flowers inversely oriented, so that the column works from below upwards. This is also true of *S. longicornu* (Fig. 4). The space between the larger corolla lobes of *S. longicornu* is relatively small, but it accommodates the movement of the column upward between the corolla lobes. Study of living material of *S. ceratophorum* (Fig. 7–9) shows that it differs from the other *Centridium* species (but agrees with the majority of *Stylidium* species) in having flowers oriented so that the column operates from above downwards. The highly distinctive pattern of the corolla lobes in *S. ceratophorum* is related to this. No other species of *Stylidium* has a pair of posterior corolla lobes bifurcate into four large cuneate divisions with forked yellow calli at their bases, and smaller pointed anterior lobes which accommodate the action of the column. On the contrary, *S. longicornu* has small, rounded posterior corolla lobes, grooved above the veins, and a pair of larger anterior corolla lobes, curiously ridged (Fig. 2, 5) and grooved, violet within (white at base of posterior lobes). The flowers of *S. ceratophorum* are large, but with a short spur; those of *S. longicornu* are small, but with a proportionately long, slender spur. The column of *S. ceratophorum* is one of the largest in the genus, that of *S. longicornu* notably small, at least for the flower size. There are no calli in the throat of *S. longicornu*.

Features of *S. longicornu* unlike any related species include the inflorescence type and the slenderness of the inflorescence. The other *Centridium* species have dichasial cymes (Fig. 7). In *S. longicornu* (Fig. 1), cymes are unilateral, with only a slight zigzag conformation betraying abortion of one of each pair of branches as the mode of origin of what must be called a raceme now in this species. There is only one raceme per plant in my material, and this raceme has a very slender axis—perhaps related to the dense restiad-grass-sedge swales in which one finds *S. longicornu*, since these inflorescences can exceed the height of these associated plants.

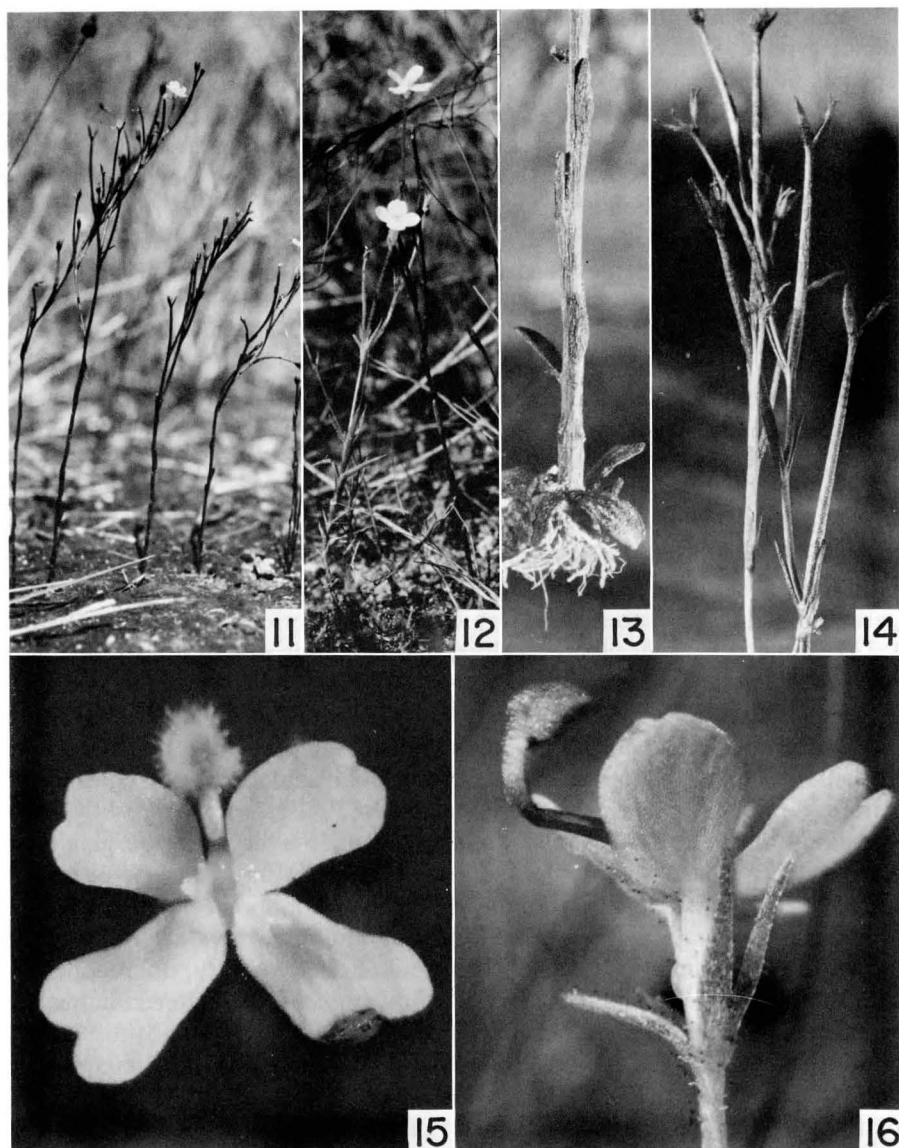
*Stylidium mitrasacmoides* Carlquist, sp. nov.

Fig. 11–16, 85

Herba annua glabra praeter calycem, saepe atropurpurascens. Folia radicalia, rosulata, lanceolata, 4–6 mm longa. Caulis 10–18 cm altus, foliis bracteaformis longe distantibus lanceolato-subulatis 2–5 mm longis instructus. Scapus solitarius, simplicis vel saepe infra floream primum ramosus. Flores ad ramos monochasia formantes sessiles distantes, bracteae infra flores binae oppositae lineares, ca. 2 mm longae. Calycis pilis glanduligeris hinc inde obsiti tubus angustissime linearis, lobi lanceolati acuti, glanduligeris, anteriores 2 usque  $\frac{1}{3}$ – $\frac{2}{3}$  fere connati, posteriores liberi vel 2 usque  $\frac{1}{3}$ – $\frac{2}{3}$  connati. Corolla alba exter pilis glanduligeris obsita lobos calycinos non superans, laciniae 4 emarginatae, rotundatae vel obcordatae, 1–2 mm in diam., albae intae. Appendices faucis 4, bifidi, aurei, nitidi. Labellum gantuse triangulari-ovatum, minutum. Columna angusta, purpurascens. Capsula linearia, 12–15 mm longa, valvis dehiscentibus a placenta recurvatum. Semina numerosissima, pallide brunnea.

Annual herb, glabrous up to the calyx (upper ovary may be glandular also), deep purple throughout except for corolla. A basal rosette of leaves present, these lanceolate, 4–6 mm long. Stem (= inflorescence axis) 10–18 cm tall, leaves bractlike, scattered along the length of the stem, subulate to lanceolate, 2–6 mm long. Scape (inflorescence axis) solitary, unbranched or often branched below the first flower. Flowers sessile, scattered along the monochasial inflorescence; bracts beneath the flowers opposite, linear, about 2 mm long. Calyx and upper ovary with scattered glandular hairs. Ovary very slender, linear. Calyx lobes lanceolate, acute, the anterior 2 united  $\frac{1}{3}$ – $\frac{2}{3}$  of their length, the posterior free or 2 of them united  $\frac{1}{3}$ – $\frac{2}{3}$  of their length. Corolla white outside, bearing scattered glandular hairs, corolla tube not exceeding the calyx lobes. The four corolla lobes are emarginate, circular in outline or somewhat obcordate, 1–2 mm in diameter, white on their inside surfaces. Throat appendages 4, bifid, golden-yellow, shining. Labellum narrowly triangular-ovate, very small. Column slender, purplish. Capsule linear, 12–15 mm long, the valves curved away from the placenta at maturity. Seeds very numerous, pale brown.





Figs. 11–16. *Styloidium mitrasacmoides* (Carlquist 15409).—11. Habit of several plants.  $\times \frac{1}{2}$ .—12. Habit of *S. mitrasacmoides* plant (upper flower) and a *Mitrasacme* plant (lower flower) growing with it.  $\times 1$ .—12. Basal leaf rosette of plant, with scalelike leaves on the elongate stem.  $\times 5$ .—14. Group of capsules.  $\times 2.5$ .—15. Flower, face view, column poised. Four bifid yellow appendages occur in the throat.  $\times 14$ .—16. Side view of flower; labellum visible at left on corolla tube.  $\times 14$ .



*Holotype*.—About one-half km northeast of Camp 1, Arnhem Land, Northern Territory. In white sand flats with *Mitrasacme*, grasses; most abundant where the soil has a crust of blue-green algae. *Stylidium schizanthum*, F. Muell., *S. lobuliflorum*, and *Helipterum* nearby. This sand flat nears scattered clumps of *Leptocarpus spathaceus* R. Br. Ovaries and calyces yellow-green at anthesis, but turning purple. Many plants in fruit as of this date. Peak flowering season this year would have been about four weeks earlier. June 4, 1978. *Carlquist 15409* (RSA). *Isotypes*.—DNA, K, PERTH, US, and others.

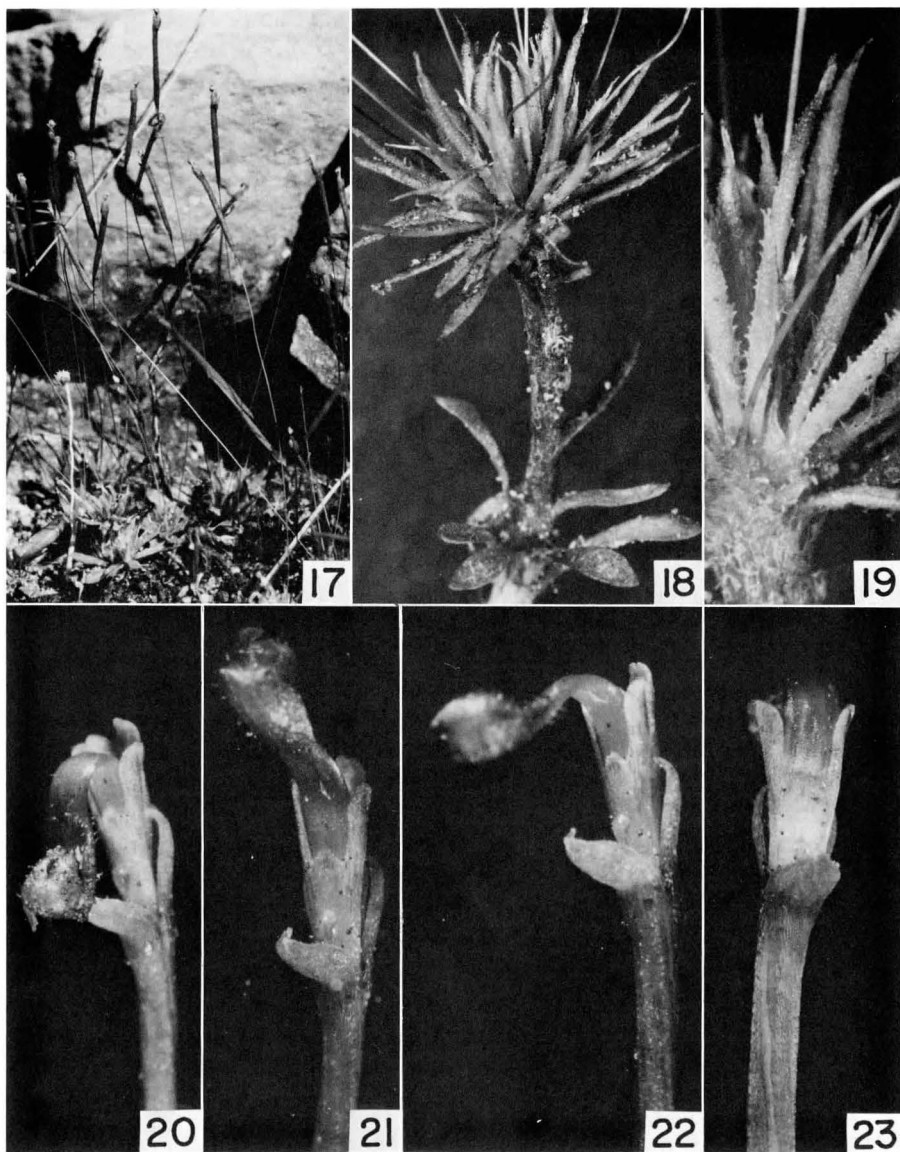
Mr. Clyde Dunlop noticed this plant midway between Camp 1 and an odd rock formation to the northeast which he nicknamed "The Anvil." This terrain contains low shelves and sandstone rises on the uphill side of which white sand has collected in pockets, so that a terracelike topography is achieved, albeit with considerable roughness owing to presence of intricately eroded sandstone. *Stylidium mitrasacmoides* is a remarkable mimic of the *Mitrasacme* with which it grows (Fig. 12). The *Mitrasacme* has white flowers of the same size as those of the *Stylidium*, and the four corolla lobes are white, with a yellow throat surrounded by yellow hairs. *Stylidium mitrasacmoides* is unusual in its genus in having four ovate corolla lobes of nearly identical size, displaced in cruciform fashion and a narrow throat with four nearly alike, bifid, yellow, dentate appendages. All of these features would represent mimicry of the *Mitrasacme*. One of the reasons why mimicry in this direction rather than the reverse may be hypothesized is that the *Mitrasacme* is widespread, whereas the *Stylidium* has been found (as of this date) only in the type locality. Other reasons are offered in a later section of this paper.

Mildbraed (1908) recognizes twelve species within the subgenus *Andersonia*. To these should be added some subsequently described species: *S. claytonioides* W. V. Fitzgerald, *S. evolutum* S. Carlquist, *S. fluminense* Erickson & Willis, *S. inconspicuum* van Slooten, *S. javanicum* van Slooten, and *S. reductum* S. Carlquist. In addition, three of the species described below must also be added to *Andersonia*. The item of significance with regard to this roster is that *S. mitrasacmoides* is quite distinctive, so that one cannot choose any one species in *Andersonia* as being closest. Consequently, there is really no purpose served by presentation of comparisons.

*Stylidium curtum* Carlquist, sp. nov.

Fig. 17–23

Herba annua. Caulis 0.5–2.0 cm altus, plerumque ca. 1.5 cm. Folia apicalia dense rosulata, lanceolato-linearia, sparse brevipilosa, apice longe acutato, mucronato, 4–8 plerumque 5 mm longa. Caulis glaber vix foliatus vel foliis paucis lanceolato-linearibus instructus. Pedicelli numerosi (2–14),



Figs. 17–23. *Styloidium curtum* (Carlquist 15473).—17. Habit of plants, type locality.  $\times 2$ .—18. Detail of plant with flattened glabrous early leaves, below; stem between rosettes, and upper, flowering rosette with subterete sparsely hairy leaves, above.  $\times 5$ .—19. Detail of upper leaf rosette to show nature of hairs.  $\times 10$ .—20–23. Closeups of flowers.  $\times 10$ .—20–22 show one flower, fig. 23 shows another.—20. Column in poised position.—21–22. Stages in repositing of column after triggering.—23. Flower with column in triggered position.

inter folia apicalia enati, graciles filiformes, glabri, stramineo-brunnei, 2–3.5 plerumque 3 cm longi, ebracteati. Calycis tubus glabrus. Calycis lobi lanceolati, 0.3–0.5 mm longi, incurvati, anteriores 2 usque ad apicem fere connati, glabri. Corollae tubus lobos calycinis aequantis, corollae laciniae minutae, rectae. Corolla roseo-pallida, sparse glanduligero-pilosa. Faux nuda. Labellum lanceolato-subulatum, acuminatum, superfice tubi paulo infra medium insertum. Columna parte basali angusta, dein ampliata marginibus retrorsum incurvatis ad  $\frac{1}{3}$  longit. retrorsum, sparse brevopilosa. Capsula anguste linearis, ca. 8 mm longa, valvis dehiscentibus a placenta recurvatis. Semina numerosissima, pallide brunnea.

Annual herb. Stem 0.5 to 2.30 cm tall, mostly about 1.5 cm. Leaves in a dense rosette at the apex of the stem; rosette leaves terete, sparsely short-pilos, provided with an acute mucronate tip, 4–8 mm, mostly 5 mm long. Stem glabrous, provided with various numbers of leaves (sometimes with a sparse second rosette of leaves at the stem base); basal leaves, if present, linear-lanceolate, flattened (Fig. 18). Inflorescences one-flowered, termed pedicels in the literature. Pedicels numerous (2–14), borne among the leaves of the apical rosette, very slender, glabrous, light brown, 2–3.5 cm, mostly 3 cm long, devoid of bracts. Ovary glabrous. Calyx lobes lanceolate, 0.3–0.5 mm long, incurved at apices, the anterior pair connate nearly to the apex, glabrous. Corolla tube equalling the calyx lobes, the corolla tube appearing quite abbreviated thereby. Corolla lobes very small, upright and not forming an expanded display. Corolla pale rose, sparsely covered with very short glandular hairs (Fig. 20–23). Corolla throat bare. Labellum subulate-lanceolate, acuminate, borne on the outer surface of the tube, below the middle of the tube. Column narrow in the basal part, but distally with a broadened incurved margin, terminal  $\frac{1}{3}$  or less of column tightly recurved; short nonglandular hairs on the distal portion of the column. Capsules narrowly linear, about 8 mm long, valves recurved away from the placenta when dehiscence occurs. Seeds very numerous, pale brown.

*Holotype*.—In sand, along wet margins of an intermittent stream. With or near *S. rotundifolium* R. Br. and *S. muscicola*. At about 6.8 km from Park Headquarters on Wilderness Trail, between turnoff to Lily Pond Trail and turnoff to Smith's Rock Trail, surface of tableland south of the Gorge, Katherine Gorge National Park, Northern Territory. June 24, 1978. *Carlquist 15467* (RSA). *Isotypes*.—DNA, K, PERTH, US, and others.

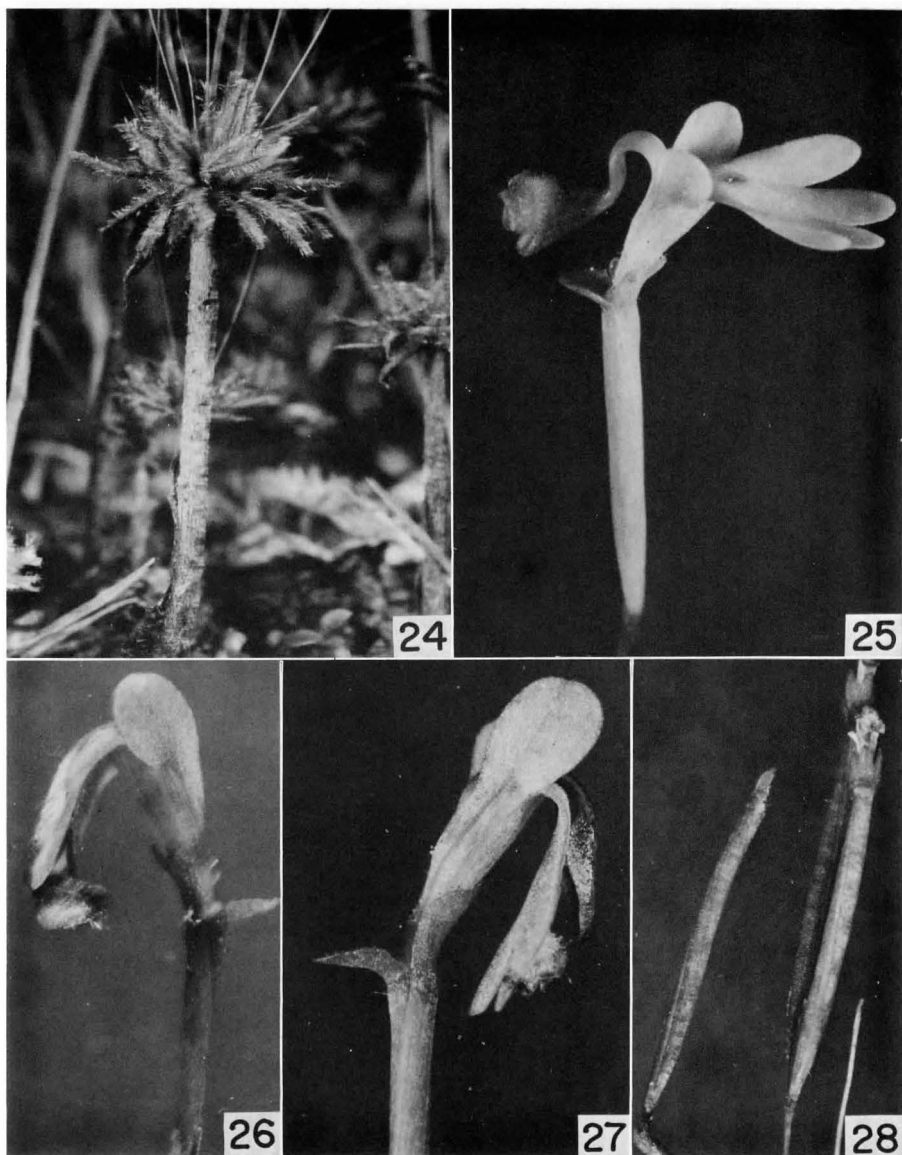
*Stylidium curtum* is clearly a member of the group of species which includes *S. trichopodium* F. Muell., *S. pedunculatum* R. Br. var. *pedunculatum* and *S. pedunculatum* var. *ericksonae* (J. H. Willis) S. Carlquist (Fig. 24–28). The photograph of *S. pedunculatum* var. *ericksonae* clearly shows differences from *S. curtum*. In *S. curtum*, the size of plants and their various organs is smaller than in *S. pedunculatum*. In *S. curtum* leaves are not densely hairy as they are in *S. pedunculatum* var. *ericksonae* (Fig. 24) or

glabrous, as they are in typical *S. pedunculatum*. The hairs on *S. curtum* leaves are not only sparse, they are shorter than those in *S. pedunculatum* var. *ericksonae*.

The most distinctive feature of *S. curtum* is the very short corolla, bearing short corolla lobes, as suggested in the species name. This corolla has a probable relation to autogamy, as described below, in simplest terms, the abbreviation of the corolla deprives potential insect visitors of a landing platform. In *S. curtum* the type of column enabling self-pollination to occur is present, as it is in *S. pedunculatum* and *S. trichopodum*. One can hypothesize that in *S. curtum* lack of attraction and of a site, correlated with length and path of column when triggered, whereby an insect can contact anthers or stigma, suggests that selfing may predominate over outcrossing by a wide margin. Corolla conformation alone suggests that return to exogamy is no longer possible. That the column still has sensitivity and operates over at least part of its expected path (Fig. 20–23), as judged from related species, suggests that acquisition of near-obligate or obligate self-pollination in *S. curtum* is relatively recent. One could say that there is no selective value (other than minor economy in energy) in maintenance of the sensitivity of the column. This contrasts with the nonsensitive column of *S. insensitivum* Carlquist (1969) in which a shift to a new pollinator has taken place. Contrary to my 1969 report of beetles, I found during my 1974 field work in southwestern Australia that *S. insensitivum* is abundantly visited by, and very likely pollinated by, quite minute flies unlike the flies that visit *Stylidium* species with sensitive columns.

Small plant size in *S. curtum* seems related to the very ephemeral wet season of the small stream where it was found. The nature of hairs on leaves is not easily interpreted, however. *Stylidium pedunculatum* var. *ericksonae* differs from typical *S. pedunculatum* only with respect to its leaf indument; thereby *S. ericksonae* J. H. Willis as a species could not be supported and was reduced (Carlquist 1978). In contrast, *S. curtum* is distinctive in a series of characteristics, even though it is related to *S. pedunculatum*.

Mildbraed (1908) calls *S. pedunculatum* and *S. trichopodum* perennials, but with question marks. Willis (1956) flatly designates "*S. ericksonae*" as a perennial. *Stylidium trichopodum* and both of the varieties of *S. pedunculatum* are annuals, however, as field studies amply demonstrate. The dense rosette surmounting the elongate stem evidently provided the problem in interpretation where a decision had to be made on the basis of dried specimens. Also the presence of one-flowered scapes in bud as well as in flower and in fruit suggests duration, but the duration is less than a year. The species of the *S. pedunculatum* group grow in depressions which become ponds during the wet season. Germination occurs underwater. As with some other aquatics, either a small basal rosette or an elongate stem, or both forms, depending very likely on depth of the water where a seed



Figs. 24–28. *Stylidium pedunculatum* var. *ericksonae*, population near Elizabeth River on Stuart Highway, S of Darwin.—24. Habit of stem and leaves.  $\times 3.5$ .—25–27. Views of flower.  $\times 10$ .—25. Flower with column in nearly poised position.—26–27. Flowers with column in triggered position.—26. Column with the second hinge locked over the edge of the corolla.—27. Column with second hinge splayed open upon face of corolla.—28. Immature capsule.  $\times 5$ .

has germinated, or events of reflooding of a pond which has dried between rains during the wet season. The stem which develops underwater bears flat, mesomorphic leaves (Fig. 18). When the stem reaches the surface of the water, the rosette of more xeromorphic, terete leaves is formed (Fig. 24). This rosette persists during the flowering season, and the size of the rosette and the number of one-flowered inflorescences formed depend on water availability. The plant dies when the sandy depression in which it grows dries. The same seasonal progression characterizes *S. floodii* F. Muell., which can be found growing with *S. pedunculatum*. In both species germination can occur when the water is very shallow. Such plants form only a short elongate stem segment, or none at all. One might expect that in these species, genetic control preventing such plants would be present: plants which germinate at the edge of a depression would dry out before flowers could form. On the contrary, plants which germinate underwater (up to about 5 cm) will be advantaged by much greater water availability.

*Stylidium curtum* may be a relatively new species, but that it has occurred at all seems related to geographical phenomena. As one goes from the coast to the interior in Northern Territory, one finds summer-wet habitats progressively smaller and shorter-lived. These habitats also are more widely spaced from each other, and population size is smaller. Segregation of distinctive populations as subspecies or species is favored by relatively small populations marked by separation from each other. Self-pollination in a population would be expected to produce moderate kinds of differentiation based on considerations comprehended in Mayr's "founder effect."

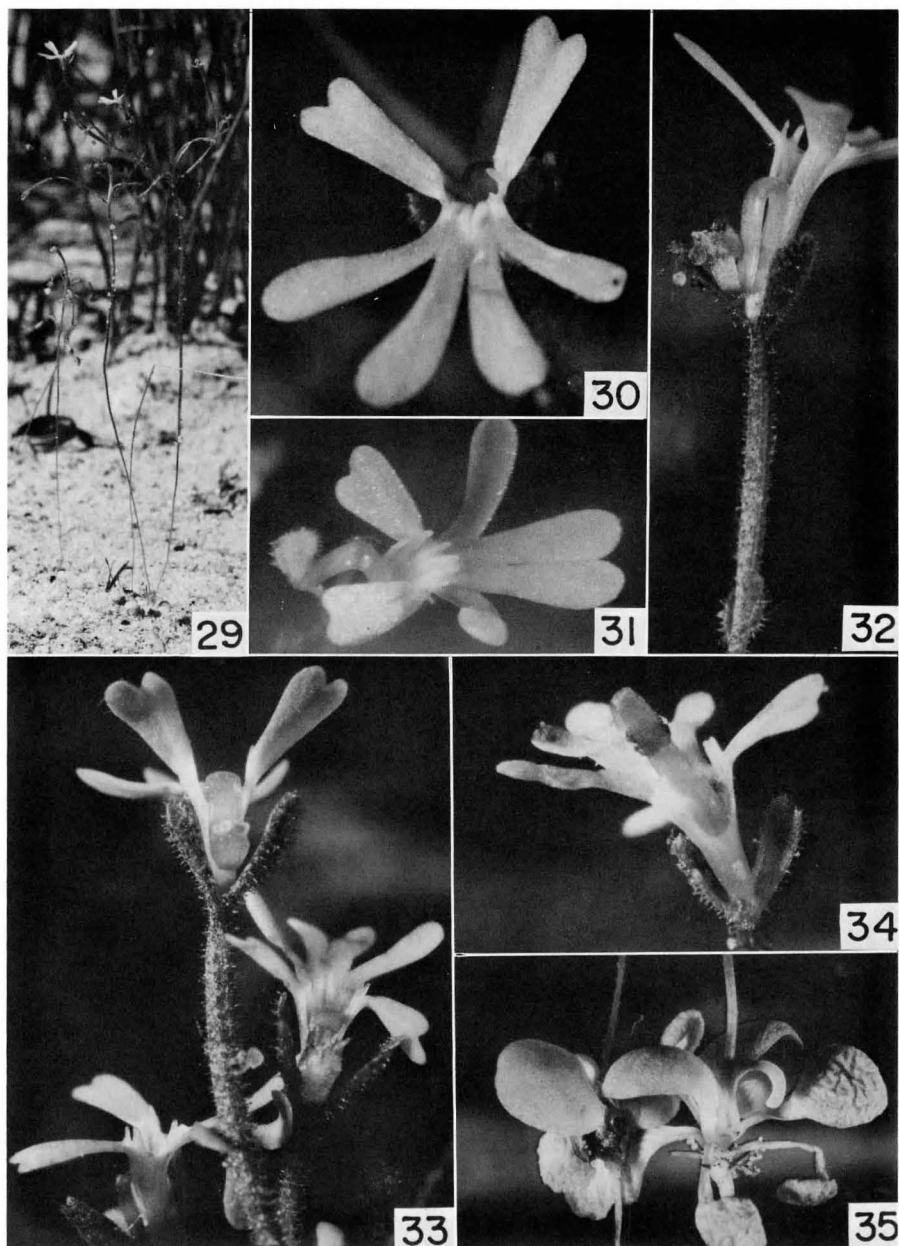
*Stylidium simulans* Carlquist, sp. nov.

Fig. 29-35

Herba annua tenella. Folia omnia basalia, rosulata, rotundata, ca. 3 mm longa, limina cupulata, hemisphaerica, brevipetiolata. Caulis filiformis, ca. 10 cm altus, pilis glanduligeris dense obsitus. Inflorescentia laxa cymosa. Calyx dense glanduloso-pubescent, calycis tubus ad anthesim 5-7 mm longus, liberis, tenellus. Calycis lobi oblanceolati rotundati, anteriores 2 usque ad apicem fere connati. Corollae laciniae subaequales, anteriores bifidae, curvatae, ca. 1.5 mm longae, posteriores emarginatae, rectae, ca. 1 mm longae. Corolla rosea pallida. Appendices faucis 2 posteriores laciniae, bifidae, anteriores 2 bifidae vel calli. Appendices faucis albae. Faux ampliata. Labellum triangulato-subulatum superficiei tubi paulo infra medium insertum. Columna ut in *S. schizantho* sed tenuior, minor. Capsula linearis, ca. 6-8 mm longa. Semina minuta, aureo-brunnea, ovoidea.

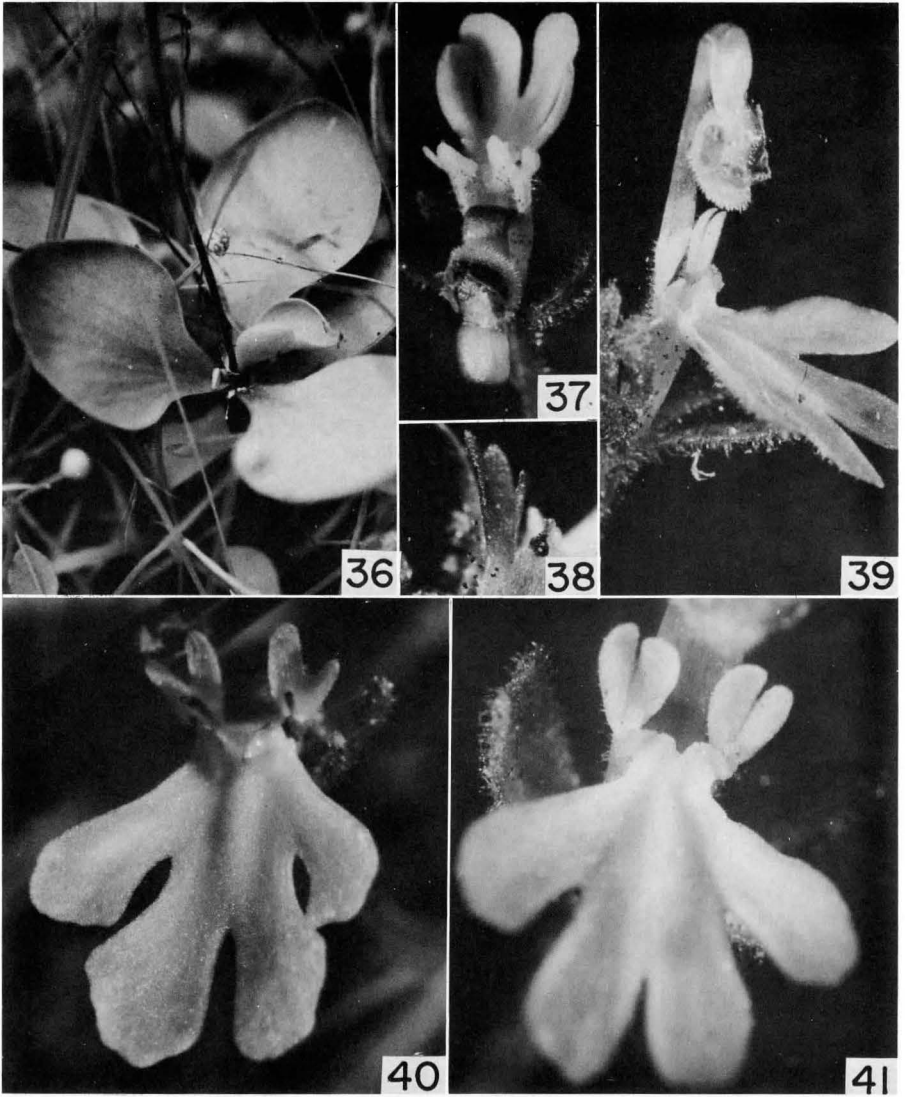
Delicate annual herb. All leaves in a basal rosette, leaves circular in outline, about 3 mm long, with a cupulate hemispherical lamina on a short petiole. Stem (=inflorescence axis) filiform, about 10 cm tall from leaf rosette to uppermost flower, densely covered with glandular hairs. Inflorescence a loose cyme. Ovary and calyx lobes densely glandular-pubescent,





Figs. 29–35. *Styliidium simulans* (Carlquist 15435).—29. Habit of plant, type locality.  $\times \frac{1}{2}$ .—30–33. View of flower.  $\times 8$ .—30. Face view of flower.—31. Slightly oblique face view of flower.—32. View of flower from side, column in poised position.—33. Three flowers; flower below left in side view; others viewed from labellum side; all with columns in poised position.—34. Flower viewed from labellum side; column in triggered position.  $\times 8$ .—35. Leaf rosettes of two plants.  $\times 5$ .





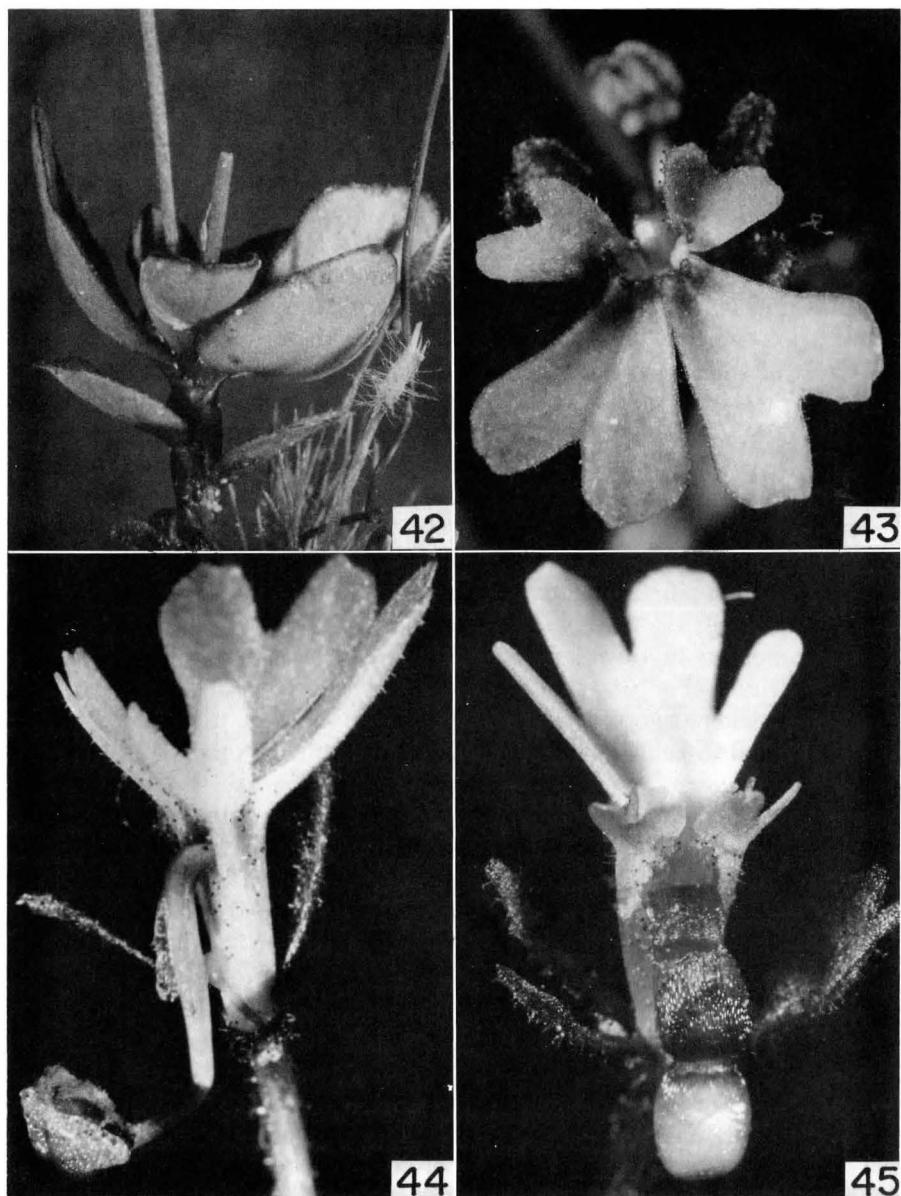
Figs. 36–41. *Stylidium schizanthum*, pictures from various populations.—35. Leaf rosette from population at Flying Fox Creek, Arnhem Highway, N.T. (Carlquist 15438).  $\times 1$ .—37–41. Closeup views of flowers.  $\times 10$ .—37. Cream-colored flower from the purple-leaved variant, near Berrimah, N.T. (Carlquist 15388).—38. Portion of flower (side view) from population 20 km S of Darwin (Carlquist 15480); "golden gland" adjacent to corner of the numeral label.—39. Flower from side, column in triggered position (Carlquist 15480).—40. Flower in face view, to show glands and teeth in throat (Carlquist 15438).—41. Flower in face view (Carlquist 15480).

ovary at anthesis 5–7 mm long, linear, slender. Calyx lobes oblanceolate, rounded at their tips, the anterior two lobes united nearly to the apex. Corolla lobes nearly alike in length, the anterior ones about 1.5 mm long, deeply bifid with curved segments; the posterior ones emarginate, straight, about 1 mm long, bifid. Corolla pale pink in color. The two posterior lobes are associated with lacinate, white, bifid, throat appendages. Anterior throat appendages are white calli, sometimes bifid and lacinate. Throat as wide as the column, as is the sinus through which the column operates. Column of the same type as in *S. schizanthum* but smaller and more slender. Capsules linear, about 6–8 mm long. Seeds minute, golden brown, ovoid.

*Holotype*.—In white sand flats, dry at this season, west of stream, with *Stylidium lobuliflorum*, *Leptocarpus spathaceus*, *Boronia lanuginosa*, *Hibbertia*, *Calythrix*, *Acacia*. At Camp 2, Arnhem Land, Northern Territory. June 8, 1978. *Carlquist 15434* (RSA). *Isotypes*.—DNA, K, PERTH, US.

*Stylidium simulans*, as the name suggests, is clearly a case of floral mimicry. It closely resembles *S. lobuliflorum* (consistently and erroneously written as "*S. lobuliferum*" by Erickson [1958]) with which it grows. Indeed, I discerned that the species were growing together only tardily, and even then I thought at first that two types of *S. lobuliflorum* were involved. Numerous details of *S. lobuliflorum* (Fig. 50–54) show that two quite different entities are involved. Indeed, *S. simulans* is more closely related to *S. schizanthum* (Fig. 36–41, 45). This is in accord with the evolutionary dictum that where two species of a genus are sympatric, they are not more closely related to each other than either of them is to other species in the genus.

Features in which *S. simulans* resembles *S. schizanthum* include a basal rosette of leaves, a loose cymose inflorescence, linear ovaries, oblong obtuse calyx lobes united nearly to the tip in the case of one pair, and a column with "instant return" capabilities. This column type will be described in detail in a later paper. In brief, the column is recurved on itself at the tip, so that a self-pollination mechanism is present (*S. simulans*: Fig. 32, 33; *S. schizanthum*: Fig. 37, 39, 45). The column, when triggered, moves to an upright position (Fig. 34, 39); instead of reposing gradually, over a period of one or more minutes, the column reposes in about a second. In *S. schizanthum*, the action of the column appears "restricted," so to speak, by the closure of the deep sinus (Fig. 45), so that the column does not traverse farther than the smaller pair of corolla lobes (Fig. 39). Cause and effect should probably be reversed, in attempting an evolutionary explanation. In *S. simulans*, however, the column operates freely, a fact which seems related to the fact that the deep sinus is free from hairs, lacinate corolla intrusions, etc. (Fig. 34). Moreover, the recurved portion of the column in *S. schizanthum* is very thick and succulent (Fig. 37, 39, 45), perhaps a device to reinforce the reflexed conformation of the column tip.



Figs. 42–45. *Stylidium muscicola* and *S. schizanthum*.—42–44. *S. muscicola* from lake near Berrimah (Carlquist 15386).—42. Leaf rosette (with *Centrolepis* plant),  $\times 2$ .—43. Flower in face view.  $\times 12$ .—44. Flower in side view, labellum visible; transparent wings on lower portion of column.  $\times 12$ .—45. *S. schizanthum* (Carlquist 15480), closeup of flower to show the recurved column in poised position; note glands occluding the sinus which surrounds the base of the column where it enters the corolla throat.  $\times 12$ .

There is no such thickening in the column of *S. simulans* (Fig. 32, 33, 34). The column of *S. simulans* is smaller than that of *S. schizanthum*, but it is also slenderer than its proportion compared to that of *S. schizanthum* would dictate.

The corolla in *S. simulans* (Fig. 30, 31) has a conformation very different from that of *S. schizanthum* (Fig. 37, 40, 41). In form, size, color, and degree of division of corolla lobes, the corolla of *S. simulans* is very much like that of *S. lobuliflorum* (Fig. 50). A casual glance can distinguish the two species with respect to the narrowness of corolla lobes in *S. simulans* (Fig. 30, 31). Moreover, the larger pair of corolla lobes are bifid into four about equally narrow and markedly curved parts—an appearance which might be easier to match in, say, *Utricularia holtzei* F. Muell. than in any species of *Stylidium*.

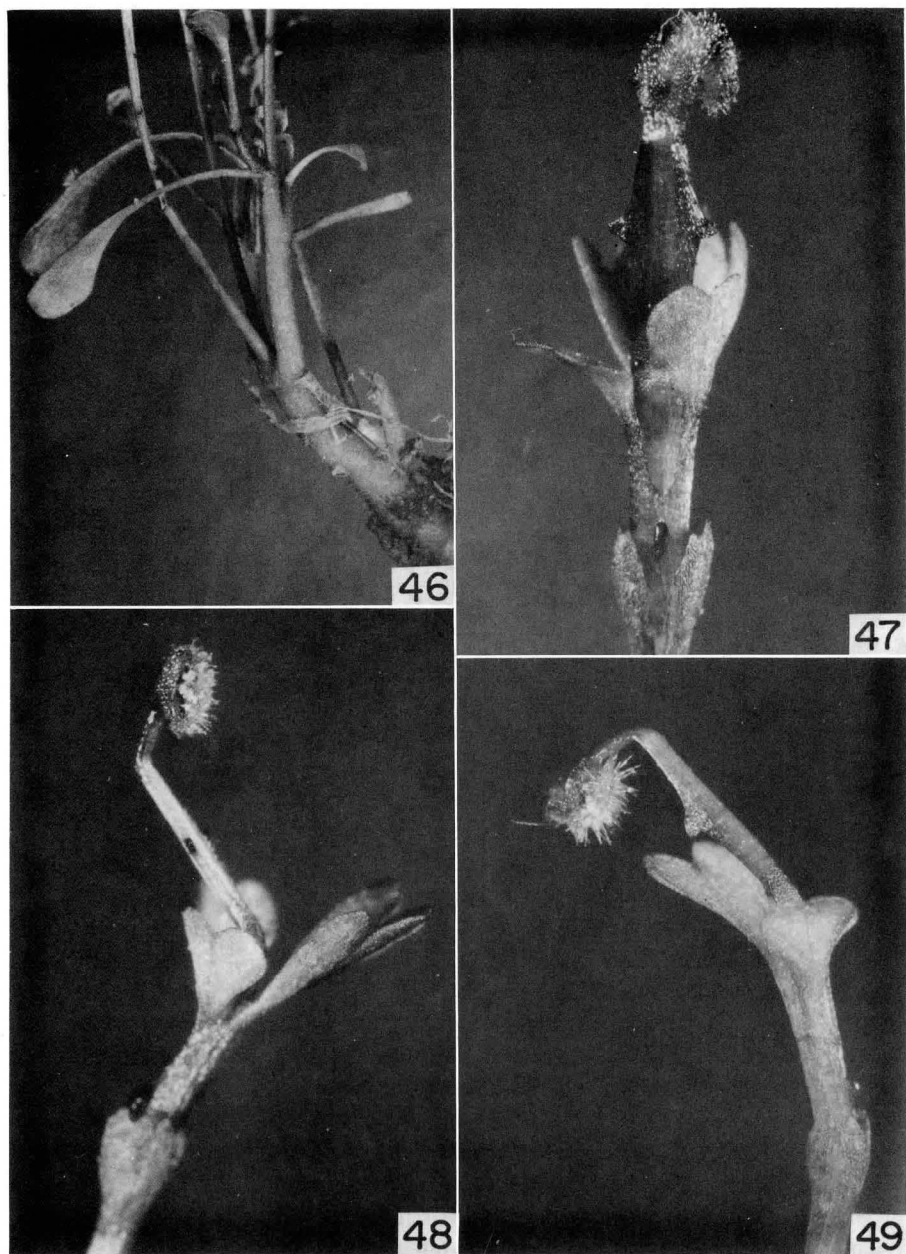
Throat appendages in *S. schizanthum* show variation. All populations of *S. schizanthum* have what have been termed “golden glands,” however. A “golden gland” may be found on either side of the corolla, in the sinus between the large and smaller corolla lobes (Fig. 38, 39, 40, 41). These glands are sometimes orange (Fig. 38, 40) rather than yellow. These golden glands also occur in all populations of *S. lobuliflorum* (Fig. 50–54). However, *S. simulans* has no golden glands. The long posterior lobes are each associated with a throat appendage bifid into two filiform teeth (Fig. 30, 31, 32, 33, 34). The anterior lobes may also be associated with such bifid teeth (Fig. 21), or these teeth may be reduced so that white calli are present (Fig. 30). These conditions are outside the variation patterns of *S. schizanthum*.

The leaves of *S. simulans* (Fig. 35) are exceptionally small and cuplike, a morphology which seemingly accords with the exceptionally dry and sunny locality where this species grows. Small leaves suffice in view of the high light intensity, and condensation of leaf form would minimize transpiration and heat absorption. Populations of *S. schizanthum* and *S. lobuliflorum* on the sandstone (Camp 1) have smaller, more condensed leaf form than do populations on the floodplain. However, leaves of *S. simulans* are smaller and more dome shaped than leaves in either of these species. Populations of *S. schizanthum* (Fig. 36–41; 45) differ appreciably. That is also true in *S. lobuliflorum* (Fig. 50–54) and *S. muscicola* (Fig. 42–44, 46–48). Is *S. simulans* just one more distinctive population of *S. schizanthum*? I feel it is well beyond that in number and kind of characteristics. It does clearly illustrate some modes of species origin in Arnhem Land, however.

*Stylidium dunlopianum* Carlquist, sp. nov.

Fig. 55–64, 84

Herba perennis. Caulis semiascendens infra sparse parceque apice rosulato-foliatus. Folia crassa, glabra, venosa supra, obovata, manifeste petiolata. Lamina 2–5 cm longa, 1–3 cm lata, petiola 1–3 cm longa. Scapi 1–4.



Figs. 46–49. *Stylidium muscicola* from stream on top of sandstone plateau, Katherine Gorge (Carlquist 15474).—46. Base of plant.  $\times 3.5$ .—47–49. View of flower,  $\times 12$ .—47. View of flower from labellum side. Note pair of teeth on column edges.—48. Flower in side view (labellum side at left); column in reposing position.—49. Flower in side view (labellum side at right), column in triggered position.

Inflorescentia ca. 20–25 cm alta, laxe cymosa, glabra praeter bracteam, pauciflora. Bracteae subulatae, 2 mm longae. Flores subsessiles, 3–4 cm longi ad anthesim. Calycis lobi in labia 2 uniti, pilis glanduligeris conspicue instructi. Calycis lobi ca. 2.5 mm longi. Corolla ca. 8 mm longa. Corollae laciniae subaequales, integrae vel emarginatae, sulcato-venosa. Corollae laciniae violaceae. Faux nuda, aurea. Corolla conspicue glanduligera exta. Labellum subulato-attenuatum. Columna permagna, papillata, infra apicem dentibus 2 latis lateralibus dilatata. Stigma magna, biloba. Capsula seminiqne ignota.

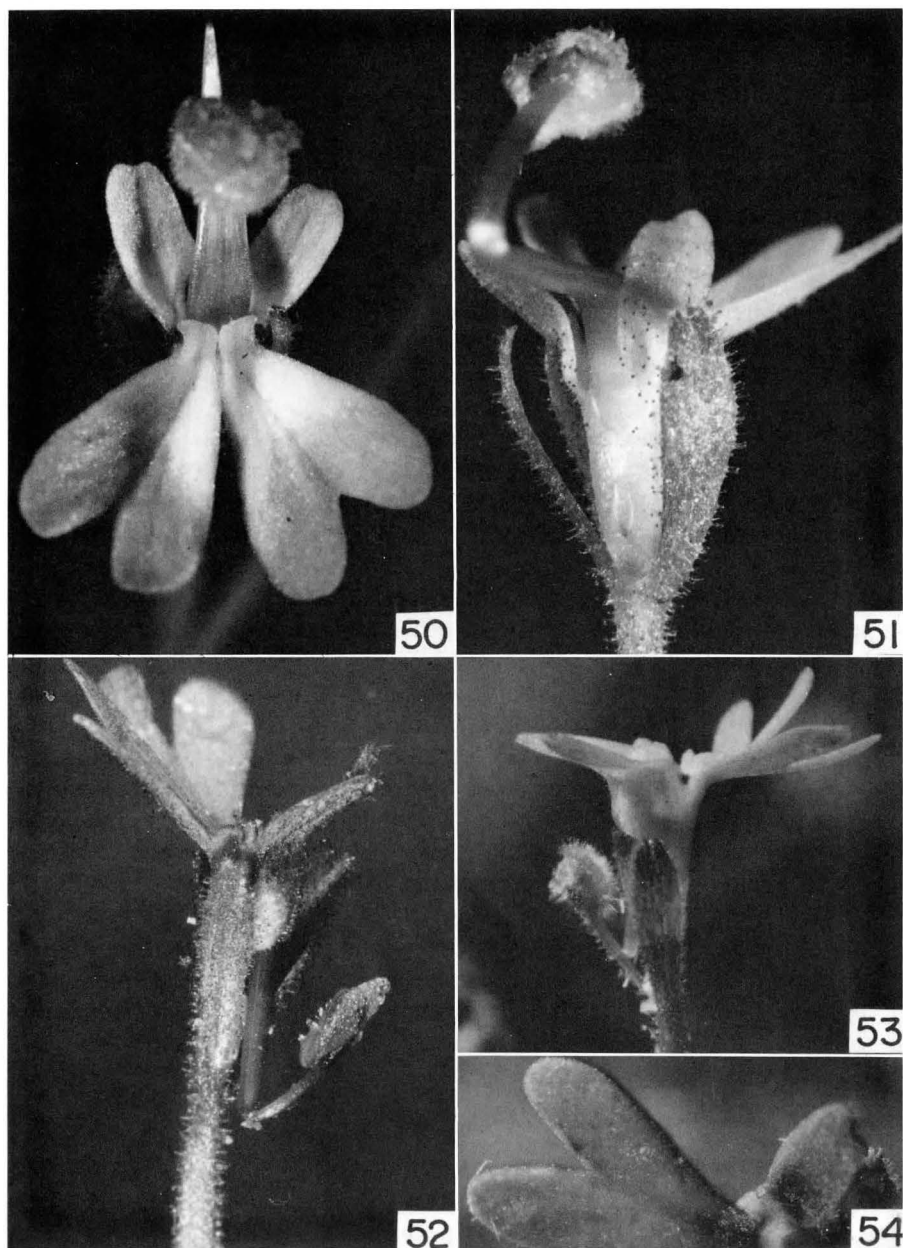
Perennial herb. Stem appears semiascending by virtue of becoming more elongate where it grows among densely tufted sedges, forming leaf rosettes at stem apices. Leaves thick, glabrous, veins apparent on upper surfaces, ovate, clearly petiolate. Lamina 2–5 cm long, 1–3 cm wide, petioles 1–3 cm long. Scapes 1–4 per leaf rosette. Inflorescence about 20–25 cm tall, a loose dichasial cyme, glabrous below the bracts, few-flowered. Bracts subulate, about 2 mm long. Flowers subsessile, about 3–4 cm long at anthesis. Ovary about 3 cm long at anthesis. Calyx lobes united into two lips, conspicuously covered with glandular hairs, especially along the margins. Calyx lobes about 2.5 mm long. Corolla about 8 mm long. Corolla lobes of about the same length, entire or emarginate, sulcate along the veins. Corolla lobes violet. Throat without appendages, golden yellow. Corolla with conspicuous but scattered glandular hairs on its outer surface. Labellum long, slender, attenuate. Column large papillate along adaxial surface distal to the sensitive hinge, with two broad teeth (enfolding anthers early in anthesis) below the apex. Stigma large, very clearly two-lobed. Capsule and seeds unknown.

*Holotype*.—Cultivated (in Darwin); originally transplanted from the edge of a permanent spring near Munmarlary Station (12°18'S., 132°36'E.), Northern Territory, in nonflowering state in May, 1978. July 21, 1978. C. R. Dunlop 4998 (RSA). *Isotypes*.—CANB, DNA, K, NT.

*Additional collection*.—In broad sedge swamp with *Drosera burmannii* Vahl, *Burmanna coelestis* D. Don, *Eriocaulon*; area adjacent to paperbark groves and stream with *Pandanus* trees along the bank, about 10 km north of Koongarra just below the sandstone scarp, Northern Territory. May 30, 1978. *Carlquist 15396* (RSA).

This species is named in honor of Mr. Clyde R. Dunlop, who, as the type collection indicates, cultivated a specimen at his home in Darwin. He established that unlike other members of the "*S. rotundifolium* complex," this plant is a perennial. The areas where this new species grows, according to him, do not dry even during the driest part of the year. In these respects, it represents *S. pachyrhizum* F. Muell. *Stylidium dunlopianum* is, in habit, to *S. rotundifolium*, as *S. pachyrhizum* is to *S. muscicola*, *S. schizanthum*, *S. leptorhizum* F. Muell., or various species of subgenus *Andersonia*. To the best of my knowledge, *S. pachyrhizum* and *S. dunlopianum* are the only perennial *Stylidiums* in the flora of Northern Territory.





Figs. 50–54. *Stylidium lobuliflorum*, closeups of flowers from several localities. All  $\times 10$ .—50. Face view of flower, column in reposing position, Camp 3, Arnhem Land (*Carlquist 15453*).—51. View of flower from labellum side, column in reposing position; flaps that enfold the poised column at its base where it enters the corolla throat are clearly visible above the



The perennial habit illustrates an adaptation quite unlike that of *S. rotundifolium*, which tends to occur on open, exposed patches of white sand, and which is ephemeral even compared to other annuals. Thus, *S. rotundifolium* (Fig. 65–70) has various sizes of leaves, but leaves are relatively small and never, in my experience show nervation on the upper surface as does *S. dunlopianum*. The variously elongate stems of *S. dunlopianum* seem correlated with ability to grow in dense sedge thickets. *Stylidium rotundifolium* apparently never has leaves borne on elongate stems.

Other distinctive features of *S. dunlopianum* (compared to those of *S. rotundifolium*) include the prominently sulcate veins of the corolla (Fig. 56, 64). The central third of the column is purple and papillate (Fig. 58, 60, 63). The stigma is clearly bilobed (Fig. 63, 64), the only *Stylidium* in which I have observed this clear expression of stigmatic dimery. There are prominent hairs between the anthers, visible before anthers open (Fig. 59). If one compares size not merely of leaves but of flowers and other portions, one finds that *S. dunlopianum* easily exceeds the range in *S. rotundifolium*. Corresponding to its wet and very likely summer-inundated habitats, *S. dunlopianum* has a flowering season later than that of *S. rotundifolium*. Plants of *S. dunlopianum* apparently do not flower prior to July; by late June, most plants of *S. rotundifolium* have completed flowering or are well advanced.

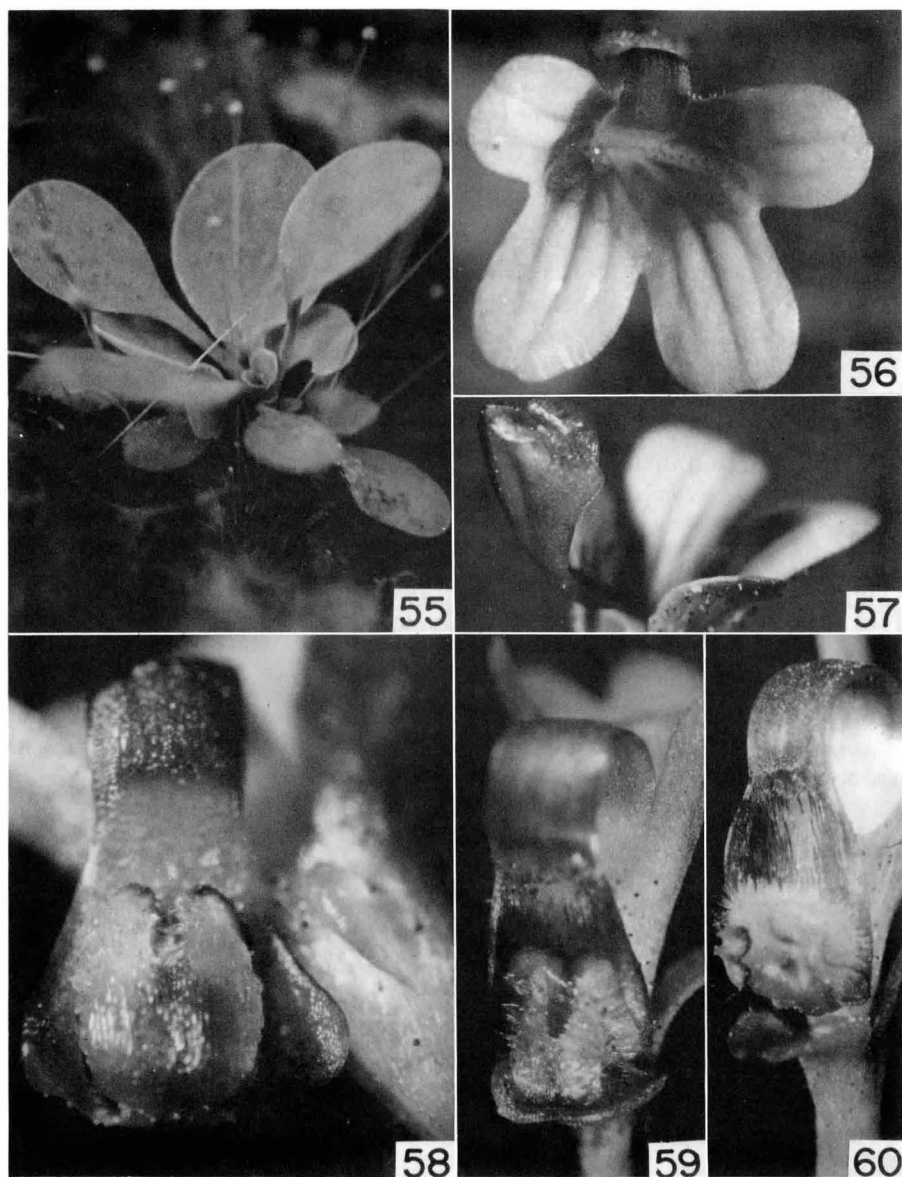
As in *S. schizanthum*, populations of *S. rotundifolium* separated by more than a few kilometers differ slightly to appreciably from each other in such features as plant size, leaf size and shape, flower size and shape, and flower and foliage coloration. As will be noted in a later section, this phenomenon seems related to the presence of self-pollination mechanisms in *S. rotundifolium*. These mechanisms are also present in *S. dunlopianum*.

*Stylidium desertorum* Carlquist.—This species was described on the basis of herbarium specimens kindly loaned by the Adelaide State Herbarium in October 1977 (Carlquist 1978). At that time I did not know I would be able to return to Northern Territory in 1978 and see living material of *S. desertorum*. An amplified description of *S. desertorum* is interjected at this point because it is relevant to a new species described below.

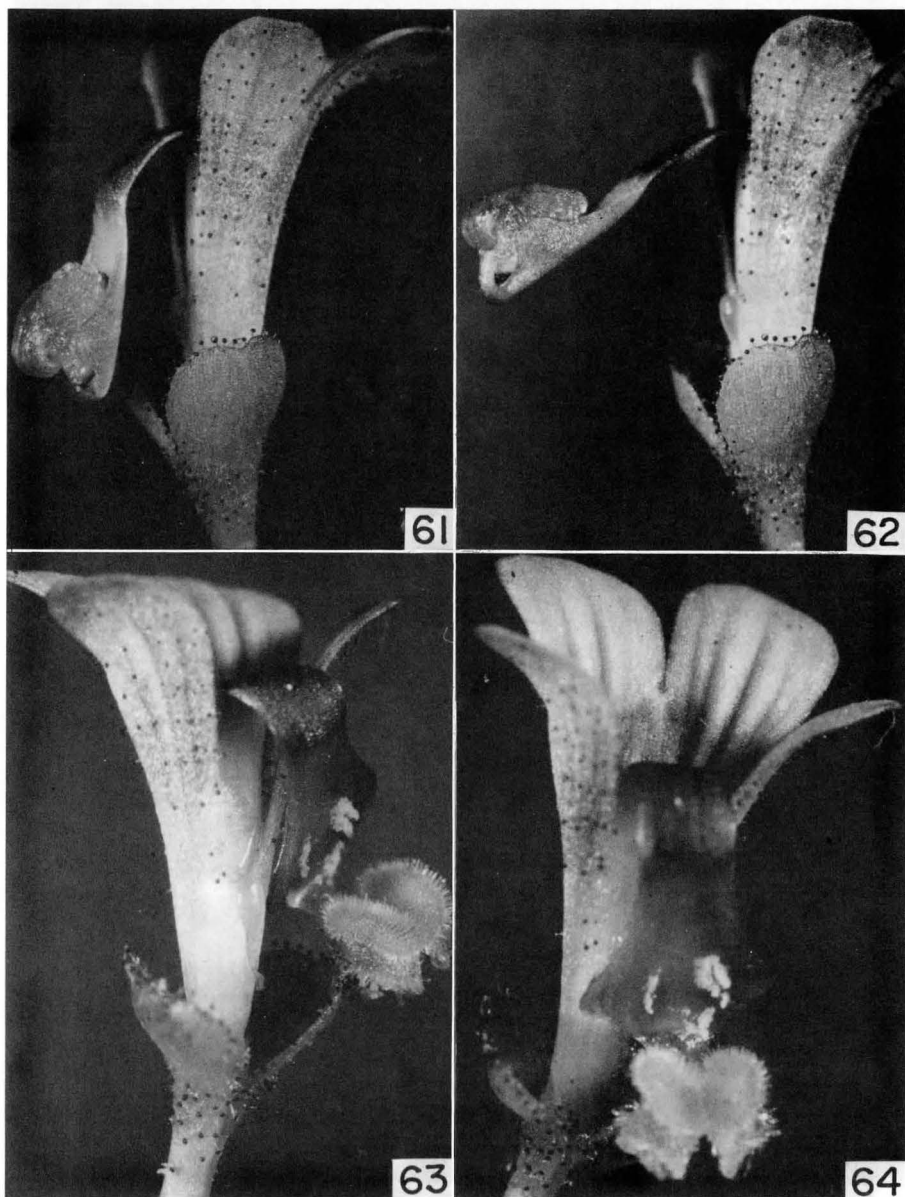
During my 1978 visit to Northern Territory I fortunately met Mr. Peter K. Latz (incorrectly cited as “D. K. Latz” at one point in my 1978 paper,

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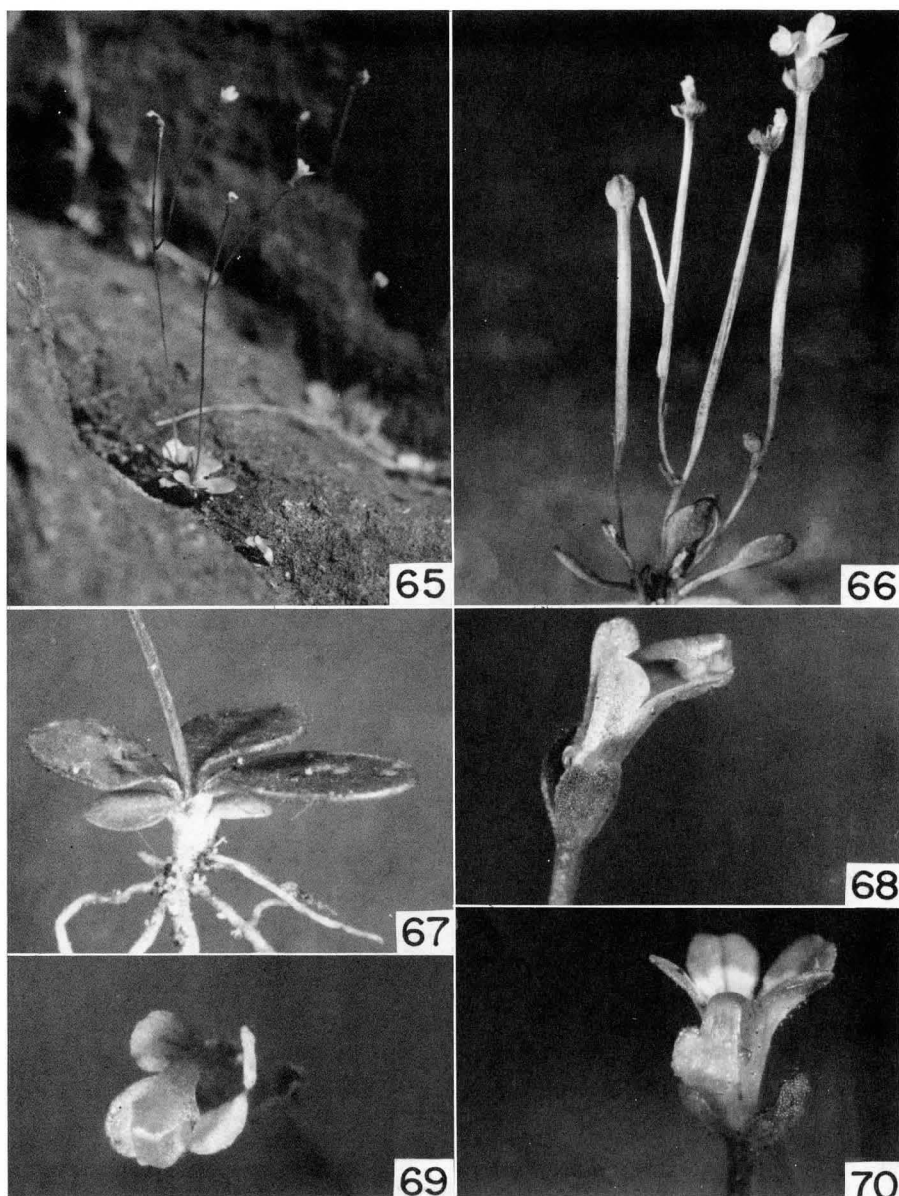
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sinus. This is a uniform species characteristic of *S. lobuliflorum* but it has been reported in no other species (Carlquist 15453).—52. Side view of flower; flaps enfolding the base of the poised column at right, below corolla lobes. From Katherine Gorge (Carlquist 15470).—53. Side view of flower, flaps (white) around column base, left, below corolla lobes. Camp 1, Arnhem Land (Carlquist 15415).—54. Half of corolla, face view. Golden gland visible at angle of sinus to right of center (Carlquist 15470).



Figs. 55–60. *Stylidium dunlopianum* (Carlquist 15396).—55. Leaf rosette,  $\times \frac{1}{2}$ .—56. Corolla, “face” view, showing corolla grooves typical of this species,  $\times 10$ .—57. Portion of flower, with column in reposing position. Flanges of the widened column form a cuplike structure.—58. View of column; margins of column show clearly. Anthers not yet open.  $\times 20$ .—59. Column similar to that of 59 showing poised column “seated” in the pair of united calyx lobes subtending it. Anthers not open.  $\times 10$ .—60. Column similar to that of fig. 59, but with the stigma fully expanded.  $\times 10$ .



Figs. 61-64. *Stylidium dunlopianum* (Dunlop 4998), the type plant. Views of two flowers from this plant, cultivated by C. R. Dunlop,  $\times 10$ .—61-62. Flower with anthers not yet open. Calyx lobes do not form a "seat" for the column.—61. Column in poised position.—62. Column reposing. Note labellum.—63-64. Flower in which stigma is fully expanded; column in poised position.—63. Oblique view of flower; labellum is long and tapered.—64. View showing broadened portion of column; pollen masses are clearly displayed; stigma markedly two-lobed.



Figs. 65–70. *Stylidium rotundifolium*.—65. Habit of plant, Camp 1, Arnhem Land (Carlquist 15413),  $\times \frac{3}{4}$ .—66. Habit of plant, Camp 3, Arnhem Land (Carlquist 15440),  $\times 2.5$ .—67. Leaf rosette (Carlquist 15413),  $\times 4.5$ .—68–70. View of flower (Carlquist 15440),  $\times 7.5$ .—68. Side view of flower, showing labellum, left, and column in triggered position.—69. “Face” view of same flower as in fig. 68.—70. View of flower with column in poised position; anthers not yet opened.

because of typographical error), who was familiar with *S. desertorum*. Before I departed from Northern Territory, he sent me living specimens of *S. desertorum* from 2-km north of the Wauchope roadhouse (20°37'S., 134°13'E.), Stuart Highway (June 21, 1978, *P. K. Latz* 7831, NT). Mr. Latz notes that this species is a biennial. I am very grateful for this living material, because by photographing it, I am able to record some features not mentioned in my 1978 descriptions. Some features, particularly those of floral conformation, cannot be preserved in herbarium specimens. I am pleased to acknowledge Mr. Latz's kind help.

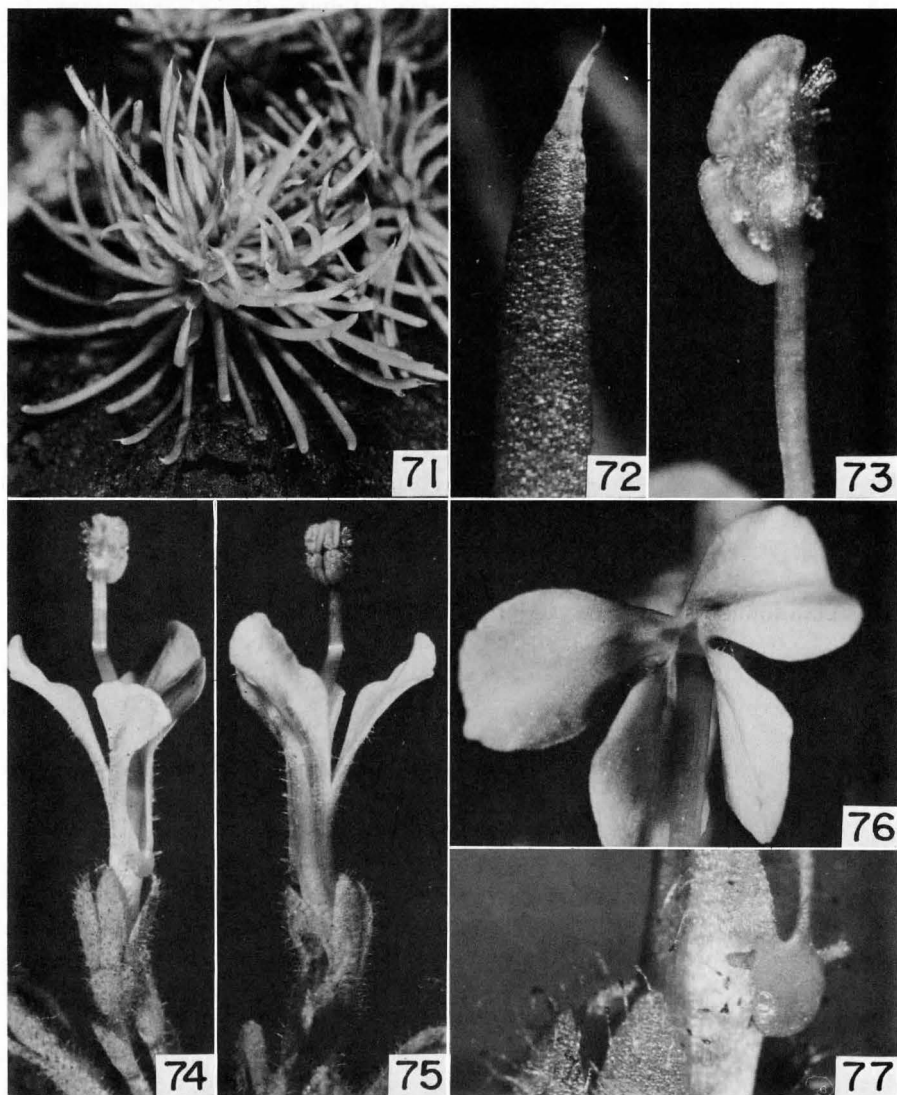
As shown in Fig. 71, the leaf rosettes of *S. desertorum* are pale green. Leaf tips (Fig. 72) show the multicellular mucro mentioned in my 1978 paper. Below the mucro epidermal cells prove to be domelike, conferring a roughened appearance to the surface. The corolla tube (Fig. 74, 75) proves to be as long as the calyx where the deepest sinus is concerned. The sinus related to the labellum is quite deep. The corolla is pale pink, slightly deeper along the middle of corolla lobes and corresponding portions of the corolla tube. Vague rose markings occur at the throat (Fig. 76). The manner in which corolla lobes are displayed is unusual, a fact noted by Mr. Latz (personal communication). The four expanded lobes are positioned somewhat obliquely rather than horizontally, so that a funnel-like form is attained. The throat features inconspicuous callus or flanges (Fig. 76). This was incorrectly termed "minutely denticulate" in my 1978 description. I also claimed that the labellum lacks appendages. In fact, it has a pair of small subulate appendages (Fig. 77). Glandular hairs on flower parts have dark tip cells (Fig. 77). The column is noteworthy in possessing vesicular hairs (Fig. 73) at its tip, a phenomenon not noted in my 1978 description.

A contrast may now be drawn between the column of *S. floodii* and *S. desertorum*. The column of *S. floodii* is flattened, broad, minutely papillate on the adaxial surface, and distinctly geniculate proximal to the anthers (Carlquist 1978, Fig. 26–27). The column of *S. desertorum* (Fig. 73–75) is slender, moderately flattened, slightly geniculate, glabrous, and smooth. As I noted (1978), *S. floodii* may bear some resemblance to *S. desertorum*, but several other species are quite conceivably as close or closer. Curiously, Mildbraed (1908) places *S. floodii* in subgenus *Tolypangium* Mildbraed, section *Floodia* Mildbraed. *Tolypangium* is mostly southwestern Australian in distribution; Mildbraed's placement should probably be reviewed. In any case, *S. floodii* and *S. desertorum* may be related to the species described below.

*Stylidium symonii* Carlquist, sp. nov.

Fig. 78–83

Herba perennis? Folia basalia, anguste linearia, 1.5–3.0 cm longa, glabra, acuta sed non mucronata. Caulis brevis, ramosus. Scapi 2–7, 4–6 cm alti,



Figs. 71–77. *Styloidium desertorum* (Peter K. Latz 7831), views of plant provided to me live by Mr. Latz.—71. Rosette of leaves,  $\times 2.5$ .—72. Tip of leaf, showing mucro,  $\times 15$ .—73. Terminus of column, illustrating two unopened anthers and vesicular hairs.  $\times 15$ .—74–75. View of a flower,  $\times 5$ .—74. Flower from labellum side.—75. Flower from side opposite labellum.—76. Face view of flower,  $\times 10$ .—77. Enlarged portion of corolla tube and adjacent calyx lobes. Labellum with its appendages is at bottom of sinus.  $\times 15$ .



inflorescentia dichasia. Bracteae infra flores lineares, oppositae, suboppositae vel alternatae. Bracteae lineares, 1–5 mm longae, glabrae. Inflorescentia dense glanduloso-pilosa. Pedicelli 1–5 mm longi, tenelli. Calycis tubus et calycis lobi dense glanduloso-pubescens. Calycis lobi ca. 1 mm longi, lanceolati, anteriores 2 connati. Corollae laciniae inaequales, posteriores parvae, anteriores magnae, erectae; laciniae anteriores bifidae. Corollae tubus et laciniae extus glanduloso-barbatae. Faux appendicibus 4 dentiformis instructa. Labellum ovoideum, exappendiculatum. Columna lata, mediane pilis glanduliferis instructa. Capsula ca. 3 mm longa, turbinata. Semina minuta.

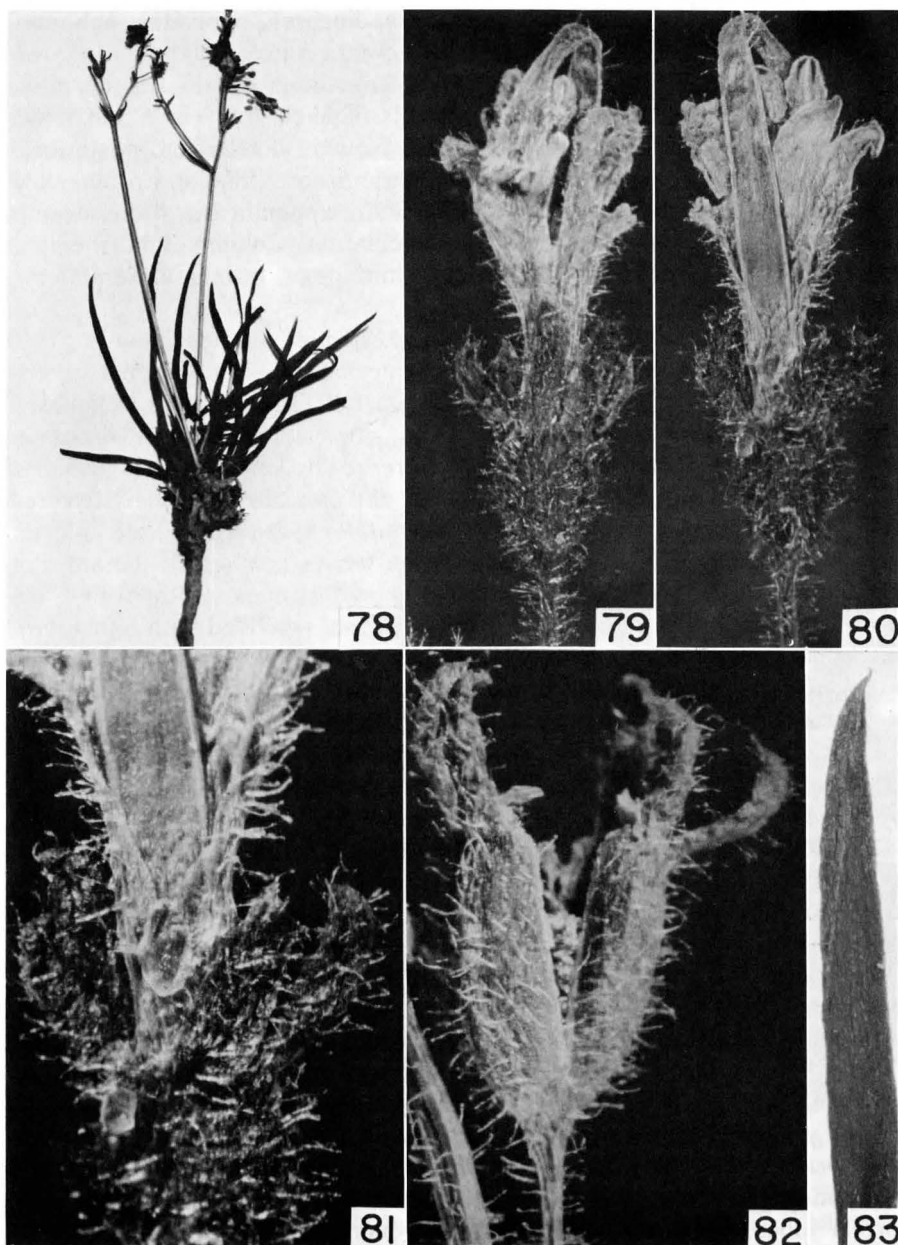
Perennial or biennial herb. Leaves basal, slender, terete, linear, 1.5–3.0 cm long, glabrous, acute but not mucronate. Stems short, branched, glabrous. Scapes 2–7 per leaf rosette, 4–6 cm tall, inflorescence a dichasial cyme. Bracts beneath flowers linear, opposite, subopposite, or alternate. Bracts linear, 1–5 mm long, glabrous. Inflorescence densely glandular-hairy. Pedicels 1–5 mm long, very slender. Ovary and calyx lobes densely covered with glandular hairs. Calyx lobes about 1 mm long, lanceolate, the anterior two connate. Corolla lobes unequal, the posterior pair small, the anterior two larger. All lobes erect. Anterior lobes bifid at apex. Corolla tube and lobes glandular-hairy on outside surfaces. Throat provided with four tooth-like appendages. Labellum ovoid, lacking appendages. Column relatively broad, provided with glandular hairs around the central portion where it is recurved. Capsule about 3 mm long, turbinate. Seeds minute.

*Holotype*.—At old B.H.P. (Broken Hill Pty.) flying field, 12°54'S., 135°28'E., Arnhem Land, Northern Territory. June 17, 1972. *D. E. Symon* 7731 (NT: sheet no. 41348).

The above specimen, once part of the Waite Agricultural Research Institute herbarium (ADW 42228) was donated by the curator, Mr. D. E. Symon, to the Alice Springs (NT) herbarium because he believed it would be more likely to receive attention there (D. E. Symon, personal communication). That did indeed prove true, for I discovered this distinctive plant when I annotated the NT specimens in late June, 1978.

One may well wonder whether description of this species on the basis of a single specimen is justified. However, the sum of characters put this specimen well beyond the limits of other known species. If one selects the two species with similarly terete linear leaves, one can make comparisons to *S. desertorum* and *S. floodii*. From *S. symonii*, *S. desertorum* differs by means of its mucronate leaves (Fig. 72), terete columns (Fig. 73–75), subequal corolla lobes, only moderately glandular-hairy (Fig. 74–76) and lack of throat appendages. From *S. symonii*, *S. floodii* differs by means of its lack of basal branching, its subglabrous scapes, the sparsely glandular nature of its flowers, its column which is wider above the middle and in which the tip is markedly recurved on the column by means of the secondary hinge





Figs. 78–83. *Stylidium symonii* (D. E. Symon 7731) (NT 41348).—78. Dried specimen, habit,  $\times 1$ .—79–80. View of a flower,  $\times 12$ .—79. View of flower from side opposite labellum.—80. View from labellum side. Two bifid larger and two bifid smaller corolla lobes present.—81. Detail of flower: labellum in center; note dense aggregations of capitate glandular trichomes.  $\times 25$ .—82. Capsule,  $\times 20$ .—83. Portion of leaf, showing acuminate tip.  $\times 8.5$ .

(bend), and its corolla lobes which are large, subequal and spreading, with fimbriate margins. Because of its curious column, *S. floodii* appears closest to *S. leptorhizum*. I compared *S. desertorum* to *S. floodii* because of P. K. Latz's annotations ("aff. *S. floodii*") on specimens of *S. desertorum*. Both *S. floodii* and *S. desertorum* seem amply distinct from *S. symonii*. The type locality of *S. symonii*, near the Goyder River in northeastern Arnhem Land, is an area as yet little explored botanically. Obviously more information about this plant would be desirable.

The status of *Stylidium pseudotenellum* O. Schwarz.—In 1927, Schwarz described *S. pseudotenellum*, based on a specimen from near Darwin. This area, now well known, should have yielded at least one collection referable to this entity if it were a distinct one, but in fact it is not. Schwarz's description is entirely in agreement with *S. fissilobium* F. Muell. He does say that *S. pseudotenellum* has a prostrate stem, but he alleges this wrongly also for *S. androsaceum* O. Schwarz, which now must be called *S. pedunculatum* var. *ericksonae*. Perennial nature of habit can easily be misdetermined when only dried specimens are studied. Schwarz (1927) compared *S. pseudotenellum* to *S. tenellum* Swartz, but he does not mention *S. fissilobium*, which evidently he neglected to study.

With the six species described above, but deducting *S. pseudotenellum*, the current total of species recognized in *Stylidium* becomes 151 (basis for this calculation discussed in Carlquist 1976, 1978). That number will doubtless change as the triggerplants become better known.

### Speciation of *Stylidium* in Arnhem Land

Obviously an account of speciation only within Arnhem Land would be too narrow. Very likely, judging from their numbers, the tropical species of *Stylidium* are centered in the sandstone plateau and the area between the plateau and Darwin. By "tropical species" one should connote essentially the subgenus *Andersonia* as delimited as Mildbraed (1908). Although Mildbraed's infrageneric systematics will doubtless be subjected to revision, only a scattering of species from subgenera other than *Andersonia* (such as two from *Centridium*, *S. ceratophorum* and *S. longicornu*) need be added to make up the roster of species in this region. Speciation in *Stylidium* of Northern Territory, then, is essentially speciation in *Andersonia*.

The habitats in Arnhem Land and vicinity are unusually favorable for occurrence of *Stylidium* and therefore for speciation. The summer wet season inundates lowland flatlands in which depressed areas of acidic white sands host *Stylidium*, along with *Utricularia*, *Drosera*, and other characteristic genera. The seasonal progression toward winter dryness may be relatively swift, but ephemeral annuals succeed under this regime—perhaps because cooler winter temperatures attenuate moisture availability and lack of frost renders winter a feasible growing season. Rainfall exceeds 50 inches

per year over the Arnhem Land–Darwin area, and the rainfall is relatively reliable (low deviation from the annual average) compared with most areas in Australia (Atlas of Australian Resources 1953).

Nevertheless, this area of Australia is not extremely favorable—indeed, other areas, such as southwestern Australia, show far greater speciation, both in *Stylidium* and in other angiosperm genera. Southwestern Australia probably has more extensive areas of acidic sand. Moreover, these sand areas are probably not as severely inundated during the wet season as are the floodplains of Arnhem Land. The favorable intermediate areas not frequently inundated nor excessively porous nor apt to rapid drying-out are probably relatively limited. On the sandstone plateau, much of the sandstone is intact, sand areas are few, or inundated by streams and rivers and then rapidly dried as watercourses contract. These features detract from the potentially favorable nature of the plateau.

The floodplain is potentially too uniform. Indeed, one may note that the ephemeral species of *Stylidium* extend, beyond Australia, from New Guinea to India, but only a few species, most of them closely related, occur within that range (Erickson 1958). Ability to germinate and grow in inundated conditions characterizes only a small number of species, and inundated areas consistently favorable for growth of ephemerals are not great in extent, in fact. The floodplains do have some favorable areas—most notably white sand areas moistened over long periods of time by underground water or flow between lakes which have underground interconnections, such as those at Berrimah. At such lakes near Berrimah, five or six species of *Stylidium* growing sympatrically may be found. Such a site is quite unusual, however.

Given the fact that central northernmost Northern Territory is a generally favorable habitat for *Stylidium*, with exceptions as noted, one must account for the fact that the area is a center for speciation in this genus, second only to southwestern Australia and clearly superior to southeastern Australia. The two concepts are not synonymous: an area can be favorable for a genus, but uniform. We must therefore account for factors which lead to a high degree of speciation in this area.

*Different kinds of favorable habitats.*—Within the area described, the following kinds of habitats may be found. Species which are characteristic of each are cited.

Sand flats, grassy but rather open: *S. schizanthum*

Grassy swales: *S. fissilobium*

Depressions (summer ponds) in white sand areas: *S. pedunculatum*

Upslope from the above depressions: *S. floodii*

In *Leptocarpus* swales: *S. ceratophorum*

Briefly wet margins of streams: *S. rotundifolium*

Shady pockets below overhanging rocks: *S. leptorhizum* (also in other habitats)

Shady wet sandy slopes: *S. cordifolium* Fitzg.

Crevices on sandstone blocks: *S. irriguum* Fitzg.

Muddy banks, depressions: *S. multiscapum* Schwarz

Very wet places, often related to streams: *S. muscicola*

This by no means exhausts the many habitats occupied by *Stylidium*, but the list illustrates that the Darwin–Arnhem Land area has variety of available habitats. One may note that among the *Stylidium*s of this area, sparse populations representing outliers from optimal areas are not infrequent, but these outliers are common enough so that in the aggregate they are worth considering.

*Isolating mechanisms.*—Australia is by no means flat, but even where topography is relatively uniform, there are significant isolating mechanisms.

A. Intervening soil types.—The localities favorable for *Stylidium* are generally white sands, which represent acidic or subacidic sandstone derivatives, unmixed with or leached of lateritic or various alkaline components. These sands usually occur in depressions, and are thus in a distribution which would be describable on a topographic map as a series of ponds and streams: in reality they are not designated as such because they are dry too much of the year. On the tableland, sand-filled depressions are even less extensive, because pockets in which sand can accumulate without sifting downslope are relatively small. The most extensive areas of sand occur where ridgelike blocks of sandstone form terraces. Rock intervenes among sand pockets on the plateau, whereas on the floodplain slight rises, sometimes composed of lateritic clays, separate sand deposits.

B. Topographic discontinuities.—On the tableland, one might think of the deep gorges as isolating mechanisms. The gorges probably have some effect, but where seed size is small, as it is in *Stylidium*, the barrier is a minor one. The gorges, although spectacular, are not wide. On more eroded eastern portions of the tableland, elevated areas are smaller, depressed areas broader. However, the tableland is lower in that area, so that the distinction between lowlands and uplands is minimal. In general, rock areas—ridges, rock-piles, slabs—serve to isolate white sand pockets. On the floodplain, dry areas, laterized or not, can be said to separate areas of summer-wet sand. Laterized areas are mostly higher than sand areas and more extensive than sand areas.

Inland from the coast rainfall diminishes. This has the effect of rendering mesic pockets smaller and less numerous toward the interior. Isolation of habitats suitable for *Stylidium* would be expected to increase in interior areas, therefore.

C. Temporal isolation.—In late June, most *Stylidium* species in Northern Territory have finished flowering. *Stylidium dunlopianum* has not begun to flower, however. *Stylidium pedunculatum* has a long flowering season. However, most species have a very brief flowering season. Late in the

season, flowering can be seen only in the most mesic spots—which thereby are more isolated from each other.

Allied to this, wet years foster more extensive populations, dry years smaller ones with more distance among them. Although rainfall seems abundant in Northern Territory, especially toward the coast, the rather drastically heavy rainfall during some storms and the marked seasonality of the climate, with a long series of dry months, means that large mesic areas in the sense of other tropical areas, are absent. Both in time and space, Northern Territory possesses a series of small, weakly interconnected populations, the desideratum for rapid evolution according to various dicta. Interconnections between populations diminish in drier years and from the coast inland. Even in wet years true continuity between populations would not be established, because conditions are not uniform across the floodplain and plateau. Most of the conditions often cited for rapid evolution of annual species can be said to be present.

D. Self-pollination mechanisms.—This topic requires extensive coverage, given below, because it is of key importance. For the moment, one may note that the widespread existence of morphological devices tending to promote self-pollination in the tropical species of *Stylidium* has the effect of increasing isolation and its effects above the levels dictated by geographical and temporal factors.

E. Population size.—This matter may be mentioned if only to illustrate it is still quite uninvestigated, not only for *Stylidium* but for other groups of plants in the Australian flora as well. Some species, such as *S. ceratophorum*, *S. cordifolium*, and *S. longicornu*, I have never seen concentrated in dense stands but such might occur in places not yet visited.

Production of dense populations is related to small seed size. Only with great abundance of seeds and therefore their smallness can dense populations be achieved in the very localized sites favorable for *Stylidium*—sites never exactly the same through successive years.

### Morphological Adaptations for Self-pollination

Before discussing the effects of pollination mechanisms on speciation patterns in tropical *Stylidium*s, the mechanisms by which various degrees of self-pollination may be achieved should be listed. The flower of *Stylidium* is basically a protandrous outcrossing mechanism. Although variations in the mechanism are both numerous and subtle, anthers typically open the first day of anthesis; they wilt and yield to the rapidly expanding stigma on the second or third day. This behavior can be seen on several of the illustrations here, as in *S. ceratophorum* (Fig. 8–10), *S. mitrasacmoides* (Fig. 15, 16), *S. muscicola* (Fig. 44), and *S. desertorum* (Fig. 74, 75). In *S. ceratophorum* (Fig. 8–10), the stigma grows out not in a cushionlike fashion

but in a columnar fashion. Such stigmas may be seen on other *Stylidium* species, such as *S. crossocephalum* F. Muell. Stigmatic hairs occur only at the apex, well away from anthers, so that self-pollination is quite unlikely to occur. The column has a sensitive hinge at the throat of the flower; there is a second bend, or hinge, however. The primary function of the second bend, or hinge is probably one of positioning the anthers or stigma for optimum pollination effect. If there were no second hinge in the column, the column surface, as well as anthers or stigma, might contact the insect; if the surface of the column hit an insect instead of the anthers or stigma, the deposition or removal of pollen would be lessened or nullified. This can be observed as a real possibility in analyses I have made by means of motion pictures. In certain species, such as *S. evolutum*, the triggering of the column is accompanied by a twisting motion near the column tip, which has the effect of broadening the area of contact. Slight modifications of the "normal" column of *Stylidium* can result in increased probability of self-pollination, but the tropical species show various degrees of morphological and phenological predispositions toward autogamy, which can be listed.

1. The stigma, rather than being on a columnar stalk when expanded, is sessile. Thus, stigmatic hairs can touch pollen grains when the stigmatic hairs expand. The anthers may have lost all pollen grains or have withered to a position where contact is no longer possible. Potentially, however, a sessile stigma can pick up pollen grains. Sessile stigmas occur in most of the Northern Territory species of *Stylidium*, and may be seen in Fig. 25, 37, 39, 48, 49, 53, 60, and 63.

2. Pollen is picked up by stigmatic hairs owing to emergence of the stigma hairs at the same time, roughly, as anthers present pollen. Obviously, the above spatial considerations must also be satisfied for temporal coincidence of stigma and anthers to result in selfing. However, temporal coincidence is no small matter in a group so strongly protandrous that anthers are initiated ontogenetically prior to other floral parts (Sattler 1973)—an unusual condition in angiosperms. Simultaneity of anther and stigma presentation is shown here for *S. muscicola* in Fig. 48. This behavior was reported for *S. alsinoides* R. Br. and *S. schoenoides* DC. by Erickson (1958). I have been able to confirm this photographically.

3. By folding of the column at the second hinge, and by widening of the portion of the column between the two hinges, a pouch into which pollen can be shed and from which the stigma can receive pollen is formed. This was mentioned by Erickson (1958) and described further by Carlquist (1969). The structure can be seen here in *S. curtum* (Fig. 20–23), *S. pedunculatum* var. *ericksonae* (Fig. 25–27), *S. simulans* (Fig. 31–34), *S. schizanthum* (Fig. 37, 39, 45), *S. dunlopianum* (Fig. 57–64), and *S. rotundifolium* (Fig. 68–70).

4. In some species, the hinge of the column tends to be held tightly in a



recurved position so that contact with a vector is potentially lessened. This position is relaxed somewhat when the stigma emerges (Fig. 25, 32, 37, 39, 60, 63, 64), but only so that the stigmatic hairs can elongate without obstruction. The degree to which the second hinge opens during the triggering process varies with the species, but it opens briefly, and during transport only, if it opens at all. Evidence can be seen in *S. pedunculatum*, in which the column becomes caught on the edge of the corolla, the second hinge folded over the margin (Fig. 26) or held splayed on the corolla surface (Fig. 27). This shows that the second hinge is momentarily opened by centrifugal force at its point of furthest advance. The recurved conformation of the column in *S. pedunculatum* is restored by reposing.

5. The second hinge of recurved columns may open out little or not at all. This appears to be true, from motion-picture evidence and other observations, in at least some populations of *S. schizanthum*. A correlative phenomenon in this species is the presence of incurved corolla lobes (Fig. 37, 45) which would impede the column; however, the column does not appear to trigger the full distance, and the maximum extent may correspond to the position shown in Fig. 39.

6. Widened column margins distal to the second hinge tend to form a pouch, furthering the probability of self-pollination. In *S. dunlopianum* (Fig. 57–64, 68–70) the widened column margins are quite conspicuous, and contain veins in addition to the two which usually can be found in a *Stylidium* column. Papillae on the adaxial column surface between the two hinges can be observed in several species (notably *S. floodii*). Papillae tend to hold pollen grains where a flower's stigma can pick them up, rather than allowing either loss or transfer via insects to other flowers.

7. Corollas may be reduced in size, relatively inconspicuous. In a sense, one could say that all the tropical *Stylidium* species have small corollas compared to those of southwestern Australia. This by itself does not indicate a lowered potential for outcrossing in the tropical species. Rather, as my field observations indicate, smaller flies visit the tropical species, so smaller flower size is to be expected. However, further diminution in the corolla size of tropical species can very easily lead to failure of insect visits, and thereby failure of outcrossing. Indeed, I have very infrequently observed insect visits to *Stylidium* flowers in tropical areas, whereas insect visits can frequently be seen in southwestern Australia.

Most populations of *S. schizanthum* have a large, horizontally expanded, purplish corolla. However, some populations of this species near Darwin have a rosette of deep red basal leaves and a yellow corolla with small, vertically displayed lobes. Not only are the corollas small, the corolla lobes are not displayed in a manner likely to serve as a landing platform—they are often cupped (Fig. 37) in these particular populations.

Within *S. muscicola*, the population shown in Fig. 46–49 suggests in small corolla size and more funnel-like shape an approach to loss of the attractive function. This is almost certainly true in *S. curtum* (Fig. 20–23). The columns in *S. curtum*, *S. schizanthum*, and *S. muscicola* must have the ability to self if corollas no longer can serve for attraction and as landing platforms. A single change such as shortening of the corolla to the point where it no longer does function in these respects can enforce self-pollination.

8. A column with recurved terminal portion may encourage self-pollination if presence of water within this fold transfers pollen grains to the stigma. Wetting may close anthers, preventing loss of pollen grains to insects. It may clump pollen grains (Fig. 63, 64: this flower was wet by rain prior to being photographed). I have observed the second hinge of columns of *S. pedunculatum* and *S. floodii* filled with water early in the morning, either from dew or from guttation. In this respect, one may note that flowering occurs in the coolest months, when dew and guttation are to be expected in wet depressed sites. This is not true in southwestern Australia, where flowering occurs at warmer times of the year.

9. In *S. floodii* (Carlquist 1978) and *S. leptorhizum*, the second hinge of the column is not tightly closed, although it is markedly recurved. This may be a progression either toward outcrossing from selfing or vice versa. These two species show a mid-point in column conformation which could easily be shifted so as to favor one modality more than the other.

10. Evolution of a less sensitive column probably results in self-pollination. *Stylidium insensitivum* (Carlquist 1969) is an exception: it achieves apparent cross-pollination without sensitive movement of the column. However, *S. reductum* (Carlquist 1978) appears to combine loss of column sensitivity with selfing. Indeed, the relatives of *S. reductum*, *S. rotundifolium*, and *S. dunlopianum*, do not reposition columns so quickly or reliably as do other *Stylidium*s. If columns transport only a single time per flower (as was observed in some plants of *S. rotundifolium*), the possibility of exogamy is limited.

### Ecological Factors Favoring Self-pollination

I have listed (1978) a number of reasons why selfing might be a favorable characteristic in tropical Australian *Stylidium*s. This list can be augmented so as to present a full picture.

1. Ephemeral habit of *Stylidium* and of other annuals produces a sudden demand for pollinators, which are probably too few.

2. Great variability in timing and abundance of flowering, products of the great year-to-year fluctuation of the monsoon climate, cannot be matched by identical fluctuation in pollinators.

3. Although flowering of the ephemerals in tropical Australia is most abundant during cool months, insect abundance is modally greater at other times of the year.

4. Annuals in this area are small and ephemeral, in accordance with the brevity of the growth season. They thereby do not form as effective a display, potentially, as can less ephemeral plants.

5. Sparse populations cannot be cross-pollinated effectively in ephemerals, and an appreciable number of populations must be described as sparse.

6. Seed abundance is selectively favored in tropical species of *Stylidium*, just as it is in desert annuals. The only effective mechanism of assuring seed abundance in small ephemeral plants, other than anemophily, is self-pollination.

The above factors do not dictate obligate autogamy. Indeed, the cost of maintaining facultative exogamy is rather small, and can be expressed merely as maintaining corolla size and pattern suitable for attraction of pollinators, as well as retention of a column capable of transmitting pollen to, withdrawing pollen from, hairs on an insect. *Stylidium curtum* appears to have crossed the threshold into obligate autogamy. Experimental work is now in progress to obtain quantitative data on autogamy in *Stylidium*.

### Speciation in *Stylidium*

If self-pollination is operating at a higher rate in tropical *Stylidioids*, they should show accordingly more rapid formation of subspecies and species. Formation of distinctive populations within the *S. schizanthum* complex was noted earlier (Carlquist 1978). To the populations cited there may be added the variant found on the sandstone plateau (e.g., Carlquist 15410). There is a very similar variant near the scarp at Flying Fox Creek, Carlquist 15438 (Fig. 36, 40). The latter variant has a rosette of large fleshy leaves (Fig. 36). These variants have bright rose-violet corolla lobes, with a pair of darker glands between the anterior and posterior corolla lobes (Fig. 40). A pair of throat appendages, displaced so as to be teeth adherent to the posterior corolla lobes, are also deeply colored and large (Fig. 40).

The *S. schizanthum* complex includes a striking variant which I have recognized as a species, *S. simulans* (Fig. 29–35). It replaces *S. schizanthum* at the type locality, and shows a close resemblance to *S. lobuliflorum*. The occurrence of the most distinctive variant in the complex, *S. simulans*, on the Arnhem Land plateau is probably significant in that a higher degree of isolation of populations there is probably basic to the speciation there.

*Stylidium muscicola* (Fig. 42–44, 46–49) forms a series of distinctive populations, both on the floodplain and on the sandstone. The nature of speciation may be viewed in terms of the two most distinctive populations and

the taxonomic problems they present. The population from wet restiad flats near Berrimah (Fig. 42–44) has stout aboveground stems with succulent sessile ovate leaves; flowers are horizontally expanded with large anterior lobes; a nearly filiform column positioned normally and of normal length; vesicular cells which form transparent wings along the column margin; and a long labellum attached very near the deep corolla sinus. The corolla and calyx are glandular-hairy in this population. A population corresponding to this was briefly and accurately described by Erickson (1958).

A quite different population of *S. muscicola* was found in small pools of residual water of an intermittent stream on the sandstone tableland of Katherine Gorge National Park (Fig. 46–49). These plants were partially submerged, and obviously had been even more inundated during their growing season. These plants have spongy stem tissue; petiolate cuneate leaves which are moderately thin; long internodes between leaves; a short inflorescence with few flowers; corollas with relatively small lobes borne in a semierect conformation; a short labellum borne on the surface of the corolla tube; a short column with two lateral teeth midway between the two hinges; a column operation over a short span, so that the column remains close to a vertical position; and a lack of glandular hairs on the calyx and corolla. If these differences were consistent one would unhesitatingly say that two species should be recognized.

However, not only are intergrades present, but these are not the only two variants in the *S. muscicola* complex. In Katherine Gorge National Park one can find plants with very broad, thin orbicular leaves, glandular-hairy flowers, and a "normal column with two wings of vesicular cells (e.g., *M. O. Parker* 799, CANB, DNA, NT). The features just listed are exceptional compared to the streambed population, and are features one finds in the Berrimah population. In some populations of *S. muscicola* the column is neither toothed nor winged, so far as can be ascertained (e.g., *N. Byrnes* & *P. Green* 2188, NT; *N. Byrnes* 2327, NT). One gains the impression that distinctive populations, adapted to various kinds and degrees of inundation and other factors, are in the process of evolving. Possibly self-pollination has played a role in maintenance of these differences—certainly autogamy is effective in perpetuating adaptive gene combinations with little change in large numbers. Some of the characters differentiating these populations may be selectively quite neutral, of course. One might guess that the small, rather funnellform corollas of the streambed population are related to self-pollination, because their minute size, lack of a landing platform, and the seemingly lessened column action that accompanies this corolla do seem diminutions of potential interaction with an insect visitor. If my speculations on the *S. muscicola* complex are accurate, appreciable separation among populations would be important in achieving isolation leading to differences. Because *S. muscicola* has the greatest preference for mesic situations—or tolerance

for inundation—of the Northern Territory Stylidiiums, greater isolation among populations would be expected than in species which grow in drier situations and therefore cover broader areas.

With respect to the taxonomic problem, I agree with Erickson's (1958) conclusion that all of the variants in the *S. muscicola* complex should be included within a single species.

The *S. pedunculatum*–*S. trichopodum*–*S. curtum* group parallels the *S. muscicola* situation. Both *S. pedunculatum* var. *pedunculatum* and *S. pedunculatum* var. *ericksonae* occur in colonies in the Darwin region. No one colony appears to contain both varieties, although distances between colonies appears to contain both varieties, although distances between colonies of the two varieties are only a few kilometers. Selfing, following infrequent dispersal events, could account for population uniformity. The most distinctive member of this species group may be *S. curtum*. It happens to grow sympatrically in the streambed on the Katherine Gorge sandstone plateau with the *S. muscicola* population described above. *Stylidium trichopodum* may be related in its distinctness to the fact that it is isolated from other species in the group; as yet it is reported only from Etheridge River in Queensland. Distinctiveness of populations in the *S. pedunculatum* group is almost certainly reinforced by self-pollination. The figures of Erickson (1958) for *S. pedunculatum* var. *ericksonae* as well as my unpublished photographs clearly show the nature of this adaptation.

In variation patterns and their geographical distribution, the *S. rotundifolium* group offers many parallels to the *S. schizanthum* and *S. pedunculatum* groups. Two of its variants, *S. dunlopianum* and *S. reductum*, have been segregated as species. However, one could say with some justification that within *S. rotundifolium* (Fig. 65–70) no two populations are alike, although populations are uniform within themselves. This pattern, as with the two species groups just discussed, seems clearly correlated with a high degree of selfing behavior related to column morphology. In fact, the *S. rotundifolium* group seems to show a greater number of devices adaptive to self-pollination than any other Stylidiiums. Because *S. dunlopianum* is a rather localized species, and unusual among tropical Stylidiaceae in being perennial, one is tempted to believe it may be derived from annuals (an adaptation to small swampy areas which never dry), and that its floral size represents a phyletic shift to larger flowers. If this has occurred, a late-season, colorful suitable for attracting pollinators could have evolved from a stock more nearly adapted to self-pollination. Flexibility in exploitation of self-pollination and cross-pollination is certainly a characteristic of many groups of herbaceous angiosperms which seem to be rapidly evolving.

The four complexes above all show their most marked diversification on and near the Arnhem Land sandstone plateau. The distinctive habitats on the plateau, juxtaposed with the floodplains near the scarp provide sharp

habitat gradients which, combined with isolating mechanisms, would tend to promote speciation. This has affected angiosperm groups other than *Stylidium*. During the 1978 visit, at least five species of *Micraria* (Poaceae) were observed. At the present moment, these are apparently undescribed. Among groups which have shown speciation on the plateau one may cite *Hibiscus*. Thus far one may cite such distinctive populations recognized as species as *H. menzelii* F. D. Wilson & N. Byrnes, and *H. symonii* F. D. Wilson & N. Byrnes. There is little doubt that an appreciable number of undescribed angiosperm species exist on the Arnhem Land plateau.

The number of species on and near the plateau is probably not remarkable, however. Other sandstone massifs are more favorable to speciation. In the case of the Guayana Highland, climatic factors are more favorable and isolation between the tablelands is greater (for a brief description, see Maguire 1971). In Arnhem Land, the lowness of the plateau means that separation by valleys does not provide severe isolation. Most of the Arnhem Land plateau falls into a 50-inch-per-year rainfall zone (Atlas of Australian Resources 1953). Although one might think the monsoons to be highly irregular, figures in that publication show that they are not, in terms of reliability of providing rainfall close to the average. Rainfall figures show the greatest irregularity in the desert regions of Australia, followed by the mediterranean-climate areas, with the least irregularity in the tropical north central part of the continent. This would seem to make this area potentially more favorable for vegetation than any other region of Australia. Northern Queensland certainly is. Northern Queensland, by virtue of the Cape York Peninsula, is least affected by the continental weather prevailing over much of Australia. More significantly, the rainfall in Northern Territory is highly seasonal (December through March), and the dryness of the remaining months quite effectively counteracts the relatively high annual rainfall total. The sandstone blocks of the plateau drain quickly and retain little water, and, in any case, are the sole rock type of the plateau. The floodplain undergoes excessive inundation. Annual totals of rain may be reliable, but much of it comes in concentrated downpours. Areas more than 300 km inland receive too little rainfall to sustain a diversity of species through a dry season, and winter frost and excessive summer heat become more prevalent at greater distances from the coast.

### Floral Mimicry

If one hypothesizes that flowers of *Stylidium* species mimic those of other angiosperms with which they grow, this concept may at first seem dubious or anthropomorphic. In fact, it is no different from the phenomenon of flowers conforming to a plan successful in attracting particular pollinators. For example, in southern California, tubular reddish flowers 2–3 cm long,



rich in nectar, may be found in a number of unrelated genera: *Beloperone* (or *Justicia*) of the Acanthaceae, *Fouquieria* (Fouquieriaceae), *Zauschneria* (Onagraceae), *Ipomopsis* (Polemoniaceae), *Delphinium* (Ranunculaceae), and *Penstemon* (Scrophulariaceae). These are all hummingbird flowers, as observations clearly indicate (e.g., Grant and Grant 1968). These genera do not mimic each other sympatrically in the same way as the *Stylidium* species described below. The principle is much the same, however: sharing a pollinator by means of similarity in floral form and color.

On the Arnhem Land sandstone, the extent of mimicry is surprising. Mr. Clyde Dunlop noticed the similarity of *S. mitrasacmoides*, described above, to the *Mitrasacme* with which it was growing. At Camp 2, Mr. Dunlop and Mr. Henshall were at first skeptical that two species of *Stylidium*, differing by a series of characters, were growing sympatrically. The superficial similarity of *S. simulans* and *S. lobuliferum* was so great that it appeared to be slightly different color forms of a single species at first glance, but the distinctions proved quite indubitable and consistent upon further examination.

During my 1967 field work in southwestern Australia, I noticed mimicry between *S. rhipidium* Erickson & Willis and *S. insensitivum* at the Cranbrook locality (Carlquist 1969). Seeing this example, I was prepared to find this phenomenon credible during my 1974 field work. The 1974 field work was undertaken in company with Dr. Larry DeBuhr, who was studying *Drosera*. He was impressed by similarity between *D. leucoblata* Benth. and *Stylidium repens* R. Br. These quite often grow together. Dr. DeBuhr found that other instances we observed in *Stylidium* represented a very real phenomenon. One can also cite an earlier observation by Rica Erickson (in Erickson and Willis, 1955). In the description of *S. xanthopis* Erickson & Willis, she claims that this new species "differs strikingly from all others in its remarkable corolla shape and colour, bearing a strong likeness to *Levenhookia leptantha*, with which it was found."

I can list the following instances from my 1974 field work in southwestern Australia in which a marked degree of resemblance was noted in my field book.

August 26, 1974. *Stylidium repens* with *Drosera leucoblata* (Carlquist 5409). Petals or corolla lobes cuneate, obtuse, white, about 5 mm long, each with a bright red spot at base. Flowers borne at same height from ground. Near Geraldton, W.A.

August 27, 1974. *Stylidium ricae* Carlquist (Carlquist 5439) with *S. petiolare* Sond. (5438) and *Drosera pycnoblata* Diels (s.n.). Flowers pink, corolla lobes or petals about 4 mm long, marked deep red at bases. Coalseam, W.A.

September 1, 1974. *Stylidium obtusatum* Sond. (5506) with *S. petiolare* (s.n.). Flowers with pale pink corollas, anterior corolla lobes 5–6 mm long,

obtuse, posterior corolla lobes shorter, all lobes unmarked. Plants at same height. Cervantes Road, east of Cockleshell Gully, W.A.

September 11, 1974. *Stylidium emarginatum* Sond. subsp. *emarginatum* with *Levenhookia pauciflora* Benth. (5600). Posterior corolla lobes white, acute, marked red at bases; anterior corolla lobes white, obtuse, 5 mm long. Red Gum Pass Road, north side of Stirling Range, W.A.

September 28, 1974. *Stylidium breviscopum* R. Br. (5828) with *Mirbelia spinosa* Benth. (5841). This resemblance may be viewed skeptically because a papilionate legume flower is so different from that of a *Stylidium*. Both are ca. 1 cm in diameter, orange on distal portions of petals or corolla lobes, red-orange in the center. The curved outline of the banner of *M. spinosa* resembles the peculiarly curved corolla lobes of *S. breviscopum*. Gardner Reserve near Tammin, W.A.

October 3, 1974. *Stylidium striatum* Lindl. (5912) with *S. maitlandianum* E. Pritzel. Both of these have corollas 8 mm in diameter, the four corolla lobes identical, flower color violet, 6 clavate teeth in the corolla throat. Mt. Leseur Rd., near Jurien, W.A.

October 9, 1974. *Stylidium expeditionis* Carlquist (5960) with *S. caricifolium* Lindl. (5966). Corolla lobes bright white, spatulate, about 7 mm long, borne about 3 dm above ground. Tutanning Reserve, near Pingelly, W.A.

October 16. *Stylidium squamosotuberosum* Carlquist with *Polypompholyx multifida* (R. Br.) F. Muell. Flowers of both are about 8 mm in diameter, the same shade of red-violet; individuals of a fly were observed going from one species to the other but not visiting other flowers at this locality. Two People Bay, W.A.

Obviously, work extending beyond mere noting of resemblances needs to be done. The sharing of a visitor (October 16 above) suggests one direction; experimental designs might also be employed. However, the following points may be hypothesized at present.

1. *Stylidium* is a large genus which suggests evolutionary expansion in recent time in its variation patterns. Floral form and color are variable features in an appreciable number of species, suggesting that variability from which patterns mimicking those of other angiosperms could be extracted does, in fact, exist in this genus.

2. If a *Stylidium* species with some floral variability is growing with a second species of *Stylidium* or another angiosperm which has a well-established relationship with a pollinator and which has little floral variability, the former species would be expected to experience rapid selection to increase the resemblance to the latter. One can hypothesize a degree of pollinator sharing prior to achievement of stable mimicry.

3. If sympatric species of *Stylidium* are involved, one would not expect them to be interfertile. Since sterility barriers are very strongly developed between species in *Stylidium* and hybrids virtually unknown (Carlquist 1969), this condition is met. Interfertility of a species pair might result in diluting, rather than enforcing, the uniformity of appeal to a pollinator.

4. Achievement of mimicry requires that both species have a fairly high degree of exogamy. The greater the exogamy, the more selective pressure would be achieved by more frequent visits by a pollinating insect.

5. The "mimicking" species, experiencing evolution toward the "model" species, must have ecological requirements virtually identical to that of the model species. Obviously no two species are precisely sympatric, but a much greater than normal degree of sympatry would be expected, and seems to be observed in the instances listed earlier. Also, a near-identity in flowering time might not be a necessity, for a model with overlap in flowering time of both species but with each flowering for part of its flowering season without the other can be shown to provide theoretically maximal resource utilization while maintaining selective pressure toward mimicry.

6. A single pollinating species, or several with the same kind of response, must be postulated.

7. The value of mimicry can be hypothesized to be greater for a species with a shorter and more intense flowering period than for a species with a long and steady flowering season, at least in the conditions present in northern Australia.

8. Species in which self-pollination is well established would be expected to show less evolution toward mimicry. Indeed, the existence of situations demonstrating mimicry in the sense described for *Stylidium* could be used as field evidence for exogamy.

9. Relatively inconspicuous flowers could not serve as models or as mimics in the sense I am indicating. Inconspicuous flowers might show conformity to a general plan (such as anemophily, or fly-pollination) but not conformity to a specific pattern exemplified by only a very few species in a given region.

10. The mimicking species might be expected often to be rather local, whereas the model species would be more widespread. Of the examples cited above, *Stylidium expeditionis*, *S. insensitivum*, *S. maitlandianum*, *S. mitrasacmoides*, *S. ricae*, *S. simulans*, and *S. xanthopis* qualify as very local species on the basis of present knowledge. That so many of the instances involve very local species can hardly be the result of chance. If the model species is more widespread than the mimicking species, the former could be a template more easily. Conformity by the fringe of a small but variable population could theoretically be expected. This fringe, altered by selection for mimicry, could well become the material from which a new species is rapidly evolved. A widespread species would not be disadvan-

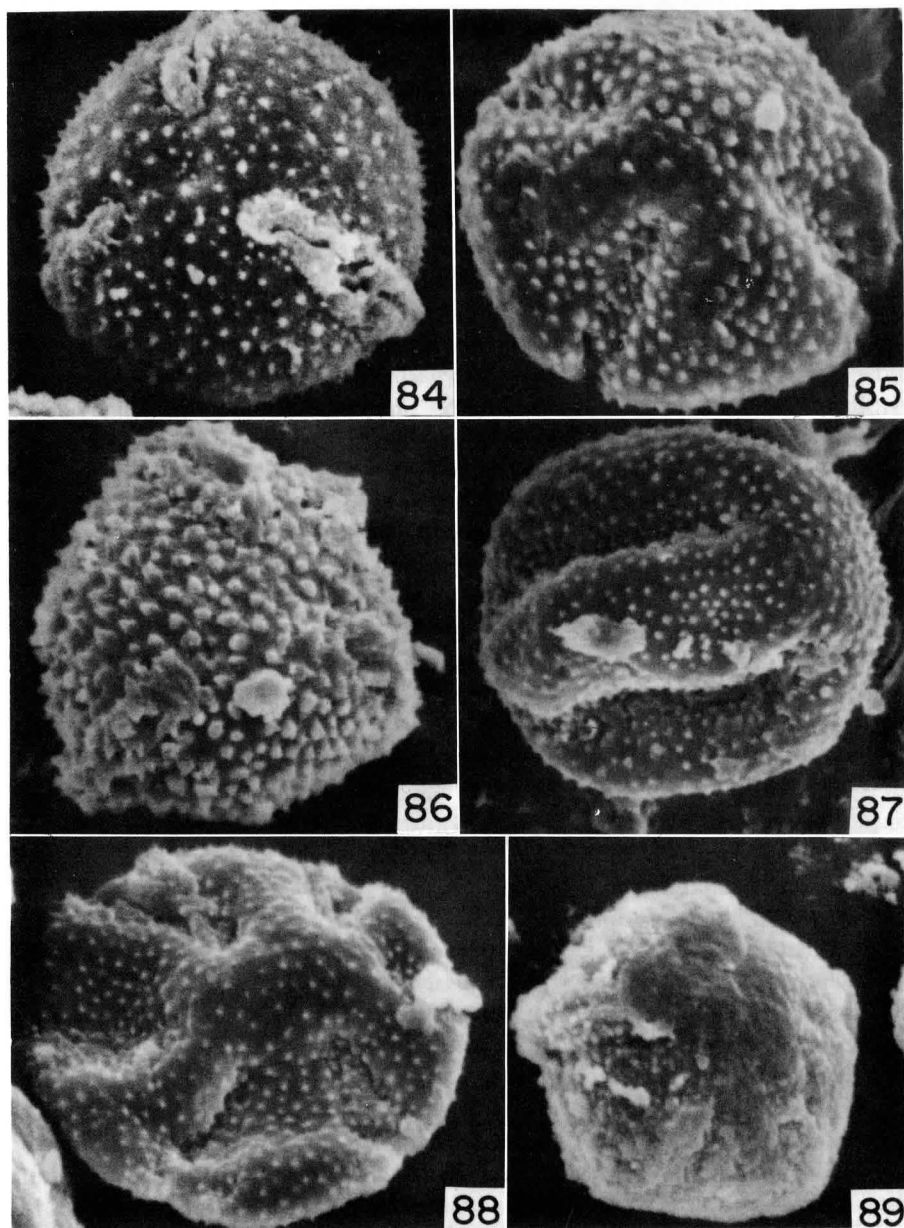
taged by sharing a pollinator with a rare species. The rare species, however, would be markedly advantaged by rapid acquisition of a well-established pollinator. It would have acquired a situation in which exogamy, regardless of population size of the mimicking species, is quite possible. If exogamy is essential to longer survivorship of a species, this type of mimicry shows how continued exogamy can occur in a small population in which high reliability of seed set is important.

### Biogeography and Evolution

The genera with more numerous primitive features for Stylidiaceae appear to be *Phyllachne*, *Forstera*, and *Oreostylidium* (Carlquist 1969). These genera do not have sensitive columns. No doubt the sequence in Mildbraed's (1908) treatment reflects this view. However, Mildbraed's sequence within the genus *Stylidium* does not appear to be a correct reading of phylogenetic descent. The subgenera listed first by Mildbraed within the genus, *Centridium* (*S. calcaratum* and allies), *Forsteropsis* Sond. (*S. imbricatum* Benth. and *S. preissii* (Sond.) F. Muell.) *Andersonia* (tropical species, mostly ephemeral, with high development of probable self-pollination mechanisms), and *Alsinooides* Mildbr. (*S. alsinoides* R. Br. and *S. tenerrimum* F. Muell., tropical and very likely specialized in numerous characteristics) are not primitive in the majority of their features. I believe that the group of three species recognized by Mildbraed as subgenus *Tolypangium* section *Sparisifoliae* Benth. seem to have the greatest number of features primitive for the genus. For example, a septum is maximally present between the two carpels. Seeds are not extremely small and numerous. Well-developed nectaries can be seen. The corolla lacks any specialized features according to any criteria advanced thus far. The stems are woody. *Stylidium laricifolium* Lindl. and *S. glandulosum* Salisb. have secondary xylem produced by a normal cambium, but interxylary phloem strands are present (data original). *Phyllachne*, *Forstera*, and *Oreostylidium* have secondary growth (Mildbraed 1908), albeit limited. Most species of *Stylidium* have a monocotyledonlike stem structure with no perceptible secondary growth. I interpret the secondary growth of *S. laricifolium* and *S. glandulosum* as a primitive feature within the genus.

Within the remainder of the genus *Stylidium*, there is little choice as to features which represent specialization for more than a few species each. However, the column modifications which suggest adaptation to facultative self-pollination seem a series of parallel specializations (Carlquist 1969). Although similar to each other in many respects, these modifications occur in quite different lines (e.g., *S. repens* and *S. pedunculatum*).

The far-south distribution of *Forstera*, *Oreostylidium*, and *Phyllachne* can hardly be overlooked. In view of today's emphasis on events of plate



Figs. 84–89. Pollen grains of *Styliidium*. Scanning electron micrographs by the author.—84. *S. dunlopianum* (C. R. Dunlop 4998). Grain tricolpate, turgid shape. Polar view.  $\times 5,000$ .—85. *S. mitrasacmoides* (Carlquist 15409). Grain tricolpate, semicollapsed. Near-polar view.  $\times 4,100$ .—86. *S. schizanthum* (Carlquist 15480). Grain tricolpate, polar view.  $\times 3,400$ .—87. *S. desertorum* (P. K. Latz 7831). Equatorial view of a tricolpate grain, grain with turgid shape

tectonics as indicative of plant distributions, a Gondwanic distribution (e.g., Schuster 1976) would naturally be suggested by some authors. However, the *Stylidium* species on the Asiatic mainland as well as in Indonesia and New Guinea show all the features one would expect for recent immigrants that arrived via long-distance dispersal. These species are reduced ephemerals, probably self-pollinating to an appreciable extent, and have such specialized features as occurrence of the labellum on the outer surface of the corolla tube rather than adjacent to the sinus. The labellum, a fifth corolla tube in *Stylidium*, is a specialized structure attached at the tube margin at the base of a deep sinus in most species of *Stylidium*. One can safely say that a corolla lobe displaced so that it is inserted not at the throat of the corolla tube but well down on the tube and on its outer surface represents a shift from the more common type. The labellum on the corolla tube surface is characteristic of some species of the subgenus *Andersonia*.

Interpretation of the Indomalaysian *Stylidium* species as recent products of long-distance dispersal from Australia should hardly be surprising, for similar long-distance dispersal has undoubtedly occurred *within* Australia. The long disjunctions between southwestern and southeastern Australia for such species as *S. brachyphyllum* Sond., *S. inundatum* R. Br., *S. beaugleholei* J. H. Willis, *Levenhookia dubia* Sond., and *L. pusilla* R. Br.—all small ephemerals with minute seeds—could hardly be interpreted in any other way. There is no reason at all for speculating, as Schuster (1976) does, that Stylidiaceae might have been in India in the Upper Cretaceous.

### Pollen Morphology

Pollen grains of six species of *Stylidium* are illustrated in Fig. 84–89. Note should be taken that magnifications differ among the photographs presented here, so that sizes are, in fact, rather different. Other differences are readily visible. Grains differ in number of colpi. The range for the genus is from three to eight (Erdtman 1952; T. Rayment in Erickson 1958). Until a greater number of *Stylidium* species are known palynologically, no statement on the distribution of colpus numbers within the subgenera can be made. At present the tricolpate condition, illustrated in three species here (Fig. 84, 86, 87) appears less common than the tetracolpate (Fig. 85), pentacolpate (Fig. 89) or hexacolpate (Fig. 88) conditions. One would assume that the tricolpate condition is basic to the family, judging from the prevalence of that colpus number in dicotyledons. Within *Stylidium*, tricolpate grains may be

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but colpi sunken.  $\times 3,400$ .—88. *S. ceratophorum* (Carlquist 15385). Near-polar view of rather collapsed hexacolpate grain.  $\times 4,300$ .—89. *S. longicornu* (Carlquist 15404). Polar view of pentacolpate turgid grain. Note psilate condition.  $\times 4,600$ .



found within the temperate species (Erdtman 1952; T. Rayment in Erickson 1958) as well as in the tropical species.

The morphological nature of colpi in *Stylidium* pollen grains present curious features. As shown in Fig. 84 and 86, some species exhibit colpi with bulging but folded surfaces. Such colpi seem different from those of pollen grains of other angiosperms. This matter needs further investigation. Whatever the covering of the colpi, conical spines tend to be present (e.g., Fig. 85) if a species characteristically has spines on the exine. In a species without spines over intercolpar areas (*S. longicornu*, Fig. 89), there are no spines over colpar areas.

Size and shape of spines on exine surface present interesting diagnostic criteria in the pollen grains. Spines can be large and conical, as in *S. schizanthum* (Fig. 86) and *S. mitrasacmoides* (Fig. 85). In *S. dunlopianum* (Fig. 84), spines are narrow, with blunt tips: this shape radiates electrons in such a way as to produce white spots in the photographic image. Medium-sized spines are found in *S. desertorum* (Fig. 87) and *S. ceratophorum* (Fig. 88). Spines are absent, or nearly so, in *S. longicornu* (Fig. 89) and *S. curtum* (not shown).

Are there correlations between pollen grain morphology and the type of column in a particular species—column recurved with adaptation for selfing vs. normal column? One would assume that echinate pollen would be correlated with insect pollination as it is in, say, Asteraceae. Stylidiaceae are well known to be pollinated by flies (Erickson 1958). Considering the rapidity of transfer of pollen from anthers to insect hairs, marked surface relief of grains to assure adherence rather than scattering might be expected. However, if the recurved column acts as a selfing device, echinate pollen surface, which would tend to retain pollen clumped where the stigma would touch it, would also have a positive selective value. Smooth grains ought to sift out of the recurved hinge more easily. Thus both exogamy and autogamy would tend to favor echinate pollen, if these considerations are correct. Indeed, there is no spine-size correlation with column morphology. Species with recurved columns have grains with large (Fig. 86), medium (Fig. 84), and no (*S. curtum*, not shown) spines. Species with normal columns have large (Fig. 85), medium (Fig. 87), or no (Fig. 89) spines. One cannot discount the possibility that oils or other substances adhering to pollen grain surfaces are present in fresh pollen and are of overriding importance. Nevertheless, one may expect that an explanation of the various spine sizes on pollen grains in the genus may yet be found.

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#### Footnote

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